

On the ecology and habitat adaptations of two intertidal spiders, *Desis formidabilis* (O.P. Cambridge) and *Amaurobioides africanus* Hewitt, at "The Island" (Kommetjie, Cape Peninsula), with notes on the occurrence of two other spiders

by

B. H. Lamoral

(Natal Museum, Pietermaritzburg)

SYNOPSIS

Four species of spiders, namely *Desis formidabilis* (Cambridge), 1890 (Amaurobiidae: Desinae); *Amaurobioides africanus* Hewitt, 1917 (Miturgidae: Amaurobioidinae); *Muizenbergia abrahami* Hewitt, 1915 (Hahniidae: Hahniinae) and *Erigonopsis littoralis* Hewitt, 1915 (Erigonidae), were found permanently inhabiting the intertidal zone of the rocky shores of "The Island," Kommetjie on the western coast of the Cape Peninsula, South Africa.

The intertidal zone of the "The Island" was surveyed and a map drawn to show the distribution of the four species. The habitats are compared. *D. formidabilis* was found to inhabit areas of the rocky shore situated between Low Water Neap and High Water Neap Tides, and *A. africanus* areas between High Water Neaps and High Water Springs. Both species were found in very large numbers. *M. abrahami* and *E. littoralis* were both sparsely distributed in areas inhabited by *D. formidabilis*.

Physical factors, behavioural adaptations and biotic factors were investigated in order to discover whether any of these are responsible for the sharp delimitation between the territories of *D. formidabilis* and *A. africanus*. Wave action was found to strongly determine the location of nest sites in both species but to be of no importance in their interspecific distribution. Selective choice of nest material, depending on the nature of mollusc shells used and the amount of exposure to wave action, is demonstrated for both. Both species are shown through measurements to make use of an equally effective physical gill and to be able to sustain prolonged immersion. Anatomical and histological investigations of the body surface, booklungs and spiracles have failed to prove the existence of a plastron. They are shown to be able to withstand an extreme condition of desiccation, and there is an indication that *D. formidabilis* is more susceptible to temperatures above 20°C. The relative humidity of their micro-habitat is shown not to vary to any significant degree. Both spiders are nocturnal and have adapted their periods of activity to tidal rhythms. The eggs of *D. formidabilis* were found to be parasitised by a Scelionid wasp belonging to a new genus and species, namely *Echthrodosis lamorali* Masner, 1968. A new species of Mesostigmatid mite belonging to the genus *Veigeiia* (Veigeiidae) was found living in and around the nests of *D. formidabilis* and *A. africanus*. In *D. formidabilis* and *A. africanus* intraspecific competition for nesting sites only becomes a problem when prospective sites are scarce. Density of populations is governed by availability of nesting sites only and not by territorial behaviour. Interspecific competition for nesting sites is very marked on territorial fringes. Experimental evidence has shown that *D. formidabilis* usually outcompetes *A. africanus*, apparently due to the fact that *D. formidabilis* has larger chelicerae, and this appears to be one of the factors controlling the distribution of *A. africanus*. Part of the diet of *D. formidabilis* and *A. africanus* together with an apparent prey selectivity characteristic of each spider are described. The latter is offered as a possible answer to the distribution of these two spiders.

CONTENTS

	<i>Page</i>
I Introduction	152
II Material	153
(a) Species investigated	153
(b) Laboratory culture method	155
III Zonal distribution of the various species and their habitat	156
(a) Locality	156
(1) Map of "The Island"	156
(2) Distribution of the spiders	156
(b) The habitats compared	160
IV Physical factors and the distribution of <i>D. formidabilis</i> and <i>A. africanus</i>	164
(a) Wave action, terrain and nest	164
(b) Immersion and its effect on respiration	166
(1) Comparative effectiveness of air films	169
(i) Respiration in air	169
(ii) Respiration in water	171
(2) Dependence on air film	174
(3) Anatomical and histological investigations relating to the above results	177
(c) Desiccation	178
(d) Temperature	179
V Behavioural adaptations to physical factors	180
(a) Hunting by night (diurnal rhythm)	180
(b) Spinning in tidal rhythm	180
VI Biotic factors influencing the distribution of <i>D. formidabilis</i> and <i>A. africanus</i>	180
(a) Associated faunas	180
(b) Prey preferences of <i>D. formidabilis</i> and <i>A. africanus</i>	182
(c) Intraspecific competition for nesting sites in <i>D. formidabilis</i> and <i>A. africanus</i>	183
(1) <i>D. formidabilis</i>	183
Mating of <i>D. formidabilis</i>	185
(2) <i>A. africanus</i>	185
(d) Interspecific competition between <i>D. formidabilis</i> and <i>A. africanus</i> for nesting sites	185
VII Discussion and conclusions	187
(a) The role of physical factors	187
(1) Wave action	187
(2) The air film	187
(i) Mechanism and comparative effectiveness	187
(ii) Resistance to prolonged immersion	188
(3) Desiccation	190
(4) Temperature	190
(5) Humidity	190
(b) the role of biotic factors	191
(1) Prey preference	191
(2) Interspecific competition for nesting sites	191
VIII Acknowledgements	191
IX References	192

I INTRODUCTION

The existence of semi-aquatic spiders is certainly not a new revelation to arachnologists, as much has been written on the habits of the fresh-water dweller *Argyroneta aquatica*; publications dealing with this species include those of Nielson (1932), Grassé, Simons et al (1949), Bristowe (1958), Savory (1964) and Levi (1967).

Bristowe (1923, 1930 and 1958) describes the habits of a few other spiders that can run under water or be submerged, such as *Lycosa pubeckensis* (Lycosidae) which lives among the halophytic plants on salt-marshes and mud-flats and "... deliberately walked down the stem of the plant beneath the surface, taking with it a bubble of air, caught by means of its hairy body." (Bristowe, 1958). Others such as *Dolomedes* (Pisauridae) and

Pirata (Lycosidae) also make temporary underwater excursions down the stems of plants, mainly using this as an escape route. *Araneus cornutus* (Argiopidae), living amongst "rushes and rank herbage in marshy grounds" (Bristowe, 1958), displays a similar behaviour. *Halotores reprobis* (Linyphiidae) is a semi-marine spider found in the epilitoral region of Britain (Bristowe, 1958) and Norway (Tambs-Lyche, 1964).

Kleemola (1963) studied the zonation of spiders on stony shores of rocky islets in the south-western archipelago of Finland. He found as many as fifty different species in various localities but unfortunately does not make it clear whether they were all intertidal. From reading his paper it seems that some species were collected above the spring high tide level.

The present investigation is a study of the ecology and habitat adaptations of four spiders, *Desis formidabilis* (O.P. Cambridge), *Amaurobioides Africanus* Hewitt, *Muizenbergia abrahami* Hewitt and *Erigonopsis littoralis* Hewitt. This study involves a determination of the zonal distribution of these animals and of the physical and biotic factors which may influence such distribution. These spiders permanently inhabit the intertidal zone on the rocky shores of Kommetjie, on the western coast of the Cape Peninsula.

II MATERIAL

(a) SPECIES INVESTIGATED

1. *Desis formidabilis* (O.P. Cambridge), 1890. In another paper appearing in this issue of the *Annals of the Natal Museum*, I have pointed out the synonymy of *D. tubicola* (Pocock), 1898, *D. pentheri* Simon, 1910 and *D. beckeri* Hewitt, 1913. Lehtinen (1967) in his revision of the cribellate spiders transferred the genus *Desis* from Agelenidae: Cybaeinae to Amaurobiidae: Desinae.

Adult females of *D. formidabilis* reach a size of 20 mm. in length when measured from the most anterior tip of the basal segment of the chelicerae to the most posterior tip of the opisthosoma. The greatest prosomal width of such a specimen is 4.0 — 4.5 mm. Characteristic of this spider are the large chelicerae (see fig. 1) directed forward, the basal segment being $\frac{1}{4}$ and the fangs $\frac{1}{8}$ of the body length as described above. The legs are long and thin, the first pair being $1\frac{1}{2}$ times as long as the total body length. Most of the body except for the dorsal surface of the chelicerae is covered with hydrofuge hairs, the density of which varies, namely many on the opisthosoma, less on the prosoma, legs and pedipalps and only a few on the maxilla. The hydrofuge hairs are of various lengths and most bear secondary processes.

Adult males of *D. formidabilis* are only slightly smaller in size than females, but are otherwise the same in appearance.

D. formidabilis is not a fully marine spider but rather a semi-marine one, because it has no adaptations enabling it to remain permanently under water. In that respect it is less aquatic than *Argyroneta aquatica*. *D. formidabilis* can submerge in well-aerated water for long periods but it must still surface to replenish its air bubble. The necessity for this will be explained later. *D. formidabilis* does not take an "air bubble" *sensu stricto* when submerging, but rather, the hydrofuge hairs covering its body prevent direct contact of the

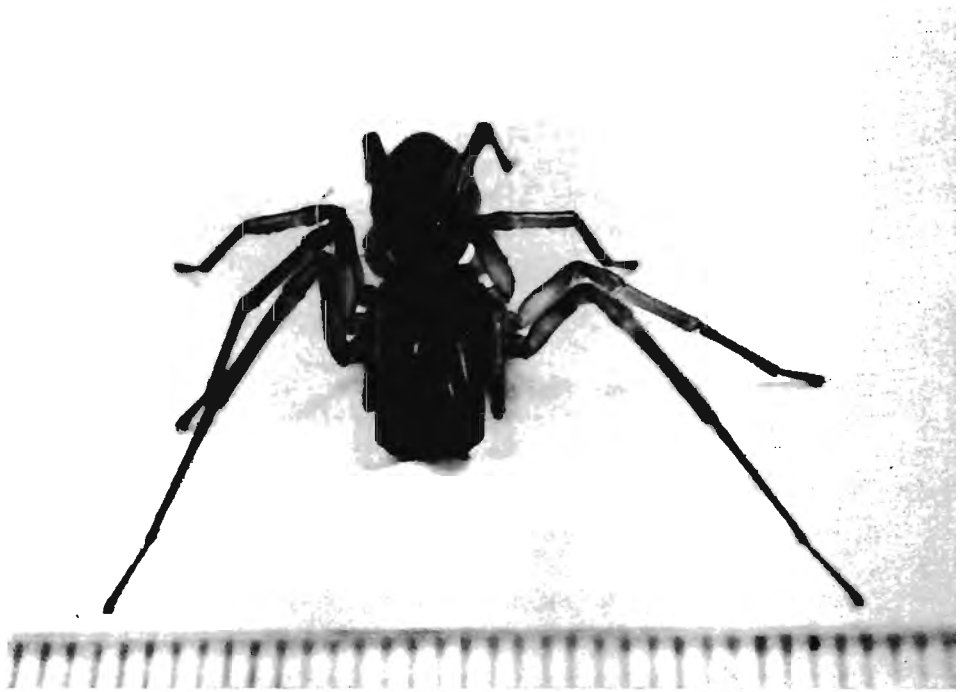


Fig. 1. Antero-dorsal (oblique) view of a female specimen of *D. formidabilis*. One division of scale = 1 mm. (Picture R. Dick)

water with the cuticular surface, thus providing the spider with a thin layer of atmospheric air around its body, to which the term *air film* might be more appropriate. It will be shown further on that this layer of air acts as a physical gill.

2. *Amaurobioides africanus* Hewitt, 1917. Hewitt (1917) placed this species among the Clubionidae. Lehtinen (1967, p.211) tentatively lists it in Miturgidae: Amaurobioidinae. Hickman (1951) synonymized all the species described, but Lehtinen (1967, p.212) has pointed out that in his opinion *A. africanus* is distinct.

A. africanus is easily distinguishable from *D. formidabilis* in its general appearance. Adult females of *A. africanus* are smaller in size than those of *D. formidabilis*. Adult females reach a total length of 16-17 mm. The greatest prosomal width of such a specimen is 3.75-4.0 mm. The chelicerae are comparatively much smaller than those of *D. formidabilis* and they are directed vertically downwards. The legs are shorter and thicker. The first, second and fourth pairs of legs are the same length as the total body length and the third pair is slightly shorter. Most of the body with the exception of the legs which have a few setiform spines on definite segments, is covered with hydrofuge hairs of the type found on *D. formidabilis*. The dorsal surface of the prosoma is covered with short grey hairs and a few scattered long black hairs, these being more numerous in the ocular region. The short grey hairs have side processes. The hydrofuge hairs of *A. africanus* enable it

to take on an air film when submerged, providing it with a physical gill as with *D. formidabilis*.

Adult males of *A. africanus* closely resemble the females but they are a little smaller. The total body length reaches 13 mm. The prosoma differs slightly in shape, being more decidedly narrowed anteriorly. Other measurements are proportionately smaller to those of the female.

Like *D. formidabilis*, *A. africanus* is not a fully marine spider, but rather a semi-marine one.

3. *Muizenbergia abrahami* Hewitt, 1915. Hewitt (1915, p. 291) placed this species in the Agelenidae: Ageleninae. Lawrence (1964, p. 33) lists it in Agelenidae: Hahniinae and Lehtinen (1967, p. 250) places it in Hahniidae: Hahniinae.

Adult females of *M. abrahami* are much smaller than those of *D. formidabilis*. Their maximum body length is 6 mm. Adult males reach a maximal body length of 4 mm. In general appearance *M. abrahami* resembles juveniles of *D. formidabilis*, but the overall body colour is darker brown. The chelicerae also project obliquely forward. *M. abrahami* was found to be far less abundant than either *D. formidabilis* or *A. africanus*. The body of *M. abrahami* is covered with hydrofuge hairs enabling it to make use of a physical gill when submerged.

4. *Erigonopsis littoralis* Hewitt, 1915. Hewitt (1915, p.295) placed this species in the Argyropidae: Linyphiinae. Lawrence (1964, p.23) lists it in his Super-family Argyropidae, family Erigonidae.

This is a small spider and it easily escapes the attention of an untrained person. It was found living in and around the nests of *D. formidabilis*. The total body length of adult females is 2.25 mm. and that of adult males is 1.75 mm. *E. littoralis* also possesses a hydrofuge system of hairs which can support an air film around its body.

(b) LABORATORY CULTURE METHODS

Two big aquaria (100 x 40 and height 30 cm.) were used to keep live specimens of *D. formidabilis* and *A. africanus* under observation in the laboratories of the Zoology Department, University of Cape Town. Stones with crevices were suitably arranged in the aquaria together with empty shells brought back from the site of collections. Most of the shells were empty limpet shells and these were positioned so as to have their concave sides fitting against the glass sides of the aquaria. Thick black paper sheets were stuck with adhesive paper against the outside parts of the aquaria to cover these sides. These paper sheets darkened the insides of the shells and could be folded back to enable observation of the spiders that had settled inside.

There were always about 3 cm. of sea water in the aquaria and high tides were simulated once or twice daily by raising the level of the water above all nests. After the appropriate interval the water was siphoned out gradually, back to the level of 3 cm. The water was permanently aerated to achieve oxygen saturation. Various intertidal animals were presented to test diet preferences.

It was found advisable to add a few drops of Methylene Blue to the sea water of the tanks to stop the growth of sulphur bacteria and other bacteria which initially fouled the

water and caused many casualties. Once this measure had been adopted, losses were minimal.

III. ZONAL DISTRIBUTION OF THE VARIOUS SPECIES AND THEIR HABITATS

(a) LOCALITY

The ecological survey of the four species was confined to the rocky shores of "The Islands" (Kommetjie), a piece of land forming a small peninsula just north of Slangkoppunt on the West Coast of the Cape Peninsula. It is surrounded on the North, West and South by the waters of the Atlantic Ocean. To the South-East of "The Island" is the "Kom," an artificial swimming pool created by the erection of a concrete wall to retain tidal waters. (See figs. 2-5).

(1) Map of "The Island"

A survey of "The Island" at Kommetjie was carried out and a map compiled by myself. Suitable criteria such as the regular occurrence of a type of Alga, and actual observations, were used to delimit the various territories inhabited by the types of spiders studied.

The zones chosen are, (also see figs. 2-5, 7):

- (i) Low Water Neaps (L.W.N.): as seen at Neap low tide level.
- (ii) High Water Neap (H.W.N.): as delimited all round "The Island" by a ribbon formed by a very small dark brown alga 1-2 mm. in length, called *Calothrix crustata* (Rivulariaceae). This belt is very striking as it imparts a dark colour to all the rocks it covers. Furthermore it makes these rocks very slippery and one has to be careful when walking across this region (see fig. 5 and 7 where one can see dark zone (H.W.N.) On the western side of "The Island" a much larger type of alga grows in this belt, viz. *Porphyra capensis* (Rhodophyceae).
- (iii) High Water Spring (H.W.S.): as determined by actual observations.
- (iv) Extreme High Water Springs (E.H.W.S.): as delimited by actual observations. (See fig. 5 and 7, E.H.W.S.).

The survey was carried out using the plane table method described by McLean and Ivimey Cook (1946). Only points A to L were surveyed for L.W.N. and points a to h for E.H.W.S. and the map only shows the area within these points. Area within a, b, c, d, e, f, g and h forms the supra-tidal fringe and consists mainly of sand and grass with a few bushes.

Dots are used in figs. 2-4 to show the relative abundance of the various types of spiders. Each dot is not a quantitative representation of the spiders. The density and number of dots merely serve to stress where the spiders are more abundant or not present at all. Abundance was recorded while collecting specimens. Not all specimens encountered were collected as this would have seriously depleted the existing populations. A considerable amount of time was spent in carefully exploring the whole intertidal area shown on the map, with a view to obtaining an overall picture of distribution.

(2) Distribution of the spiders.

- (i) *D. formidabilis*: was only found in the zone extending from L.W.N. to H.W.N. (dark brown belt). The delimitation, especially near H.W.N., is sharp (see fig. 2).
- (ii) *A. africanus*: was only found in the zone extending from H.W.N. to H.W.S. The density of specimens being greatest in the lower half of this zone. see (fig. 3).



Fig. 2 Map of The "Island", Kommetjie, showing the distribution of *D. formidabilis* during March, April and May 1966. (See text for further explanations.)



Fig. 3. Map of "The Island", Kommetjie, showing the distribution of *A. africanus* during March, April and May 1966. (See text for further explanations.)

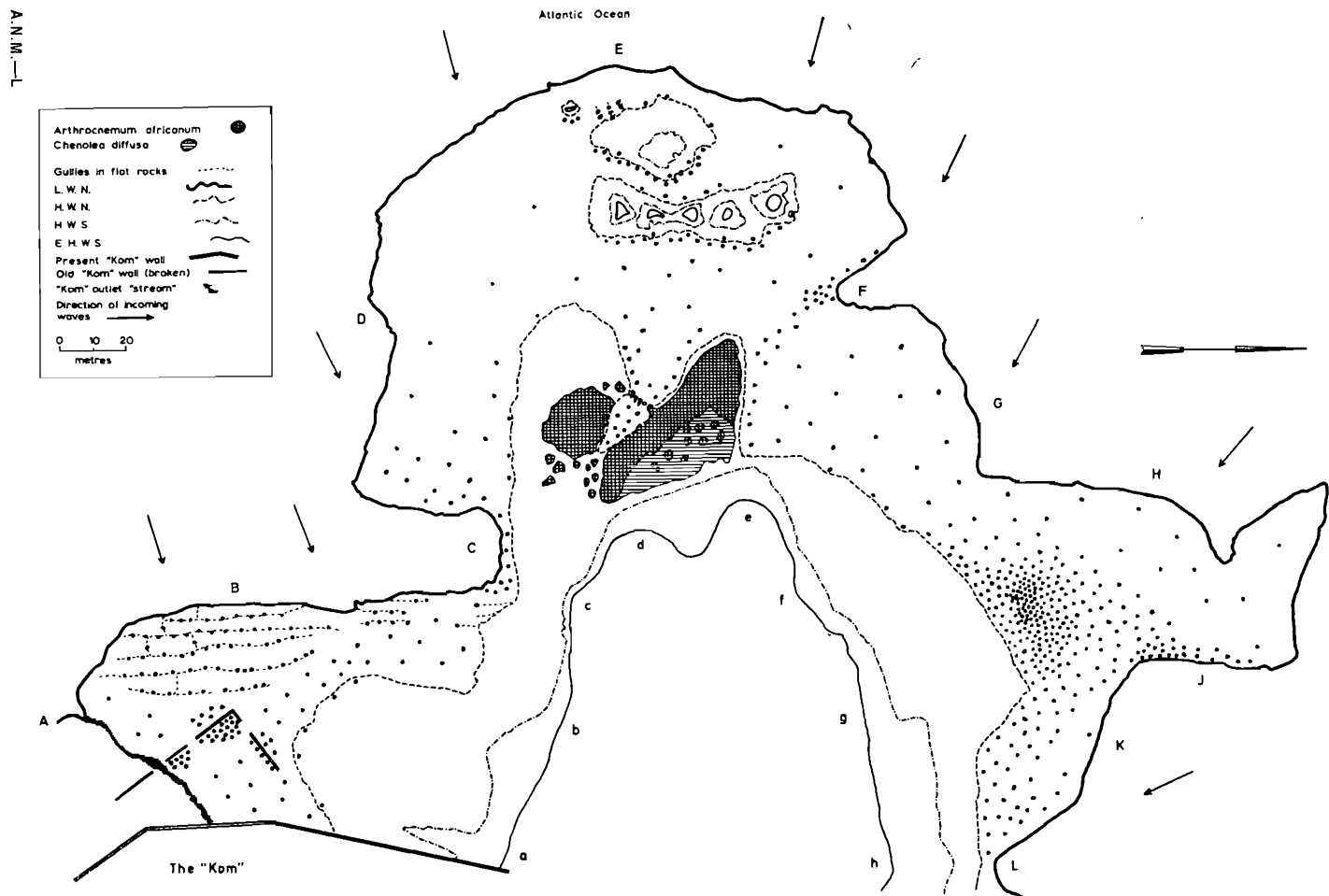


Fig. 4. Map of "The Island", Kommetjie, showing the distribution of *M. abrahami* i.e. + and *E. litorali* i.e. ● during March, April and May 1966. (See text for further explanations).

- (iii) *M. abrahami*: was found mainly in the region overlapping H.W.N. Specimens were only found on the northern side of "The Island" (see fig. 4).
- (iv) *E. litoralis*: was found in the same region as *M. abrahami* with the exception of some specimens that were found on the western and part of the southern side of "The Island." *E. litoralis* was found mainly in association with *D. formidabilis* (see fig. 4).

(b) THE HABITATS COMPARED

Most of the intertidal zone can be described as a typical rocky shore. Many loose rocks of various sizes alternate with regions of big, flat, eroded slabs of rocky substratum (see figs. 5, 6 and 7). Points to note are: (See fig. 2-4).

- (i) No spiders settled on the side East of the new "Kom" wall as the water level never drops here.
- (ii) The old "Kom" wall affords good shelter against wave action and accordingly many spiders settled behind it.
- (iii) Presence of what has been termed gullies in flat rocks along region A B C of fig. 2. These gullies also afford good protection against wave action as demonstrated by the fact that most spiders settled in gullies that run at a right angle to the direction of the incoming waves.
- (iv) Presence of two large beds of *Arthrocnemum africanum* and *Chenolea diffusa* (Both Angiosperms, Dicotyledons, Chenopodiaceae) situated West of points d in fig. 2. The smaller bed consisting mainly of the former and the larger bed of both types.
- (v) The region, well sheltered from wave action, between H.W.N. and H.W.S. in area between points C and D in fig. 2-4. Part of this region can be seen in fig. 6 (encircled by a broken line). When the tide rises, water does not come up easily from point C but rather most of it comes from the area between points D and F and goes up the channels between the two main beds of *Chenolea* and *Arthrocnemum*.

That there is a barrier checking strong water influx from point C is supported by the fact that dead kelp was found to pile up immediately North of point C (see fig. 6, arrow head points to kelp deposited). Most of this area is covered by loose roundish rocks and stones lying on top of each other with a coarse sand substratum in certain parts.

- (vi) Raised portions on western side of "The Island" caused by the presence of very large rocks (almost boulders). Some gullies are also present on the western side of most the westernly placed raised portion. It is interesting to note here that where there are normally few spiders present in the western area of "The Island," we have, however, a greater density on the sheltered side of the western raised portions.
- (vii) From F to L the area occupied by *D. formidabilis* is formed mainly of loose rocks lying pell-mell. No gullies are present but these rocks nevertheless afford good shelter inasmuch as they contribute a lot in breaking wave action (see fig. 7). The area occupied by *A. africanus* parallel to this has less loose rocks and more large flat rocks with crevices in them.



Fig. 5. Intertidal area West of the "Kom." Picture taken from a spot slightly North of point b in fig. 2. a, new "Kom" wall; b, old "Kom" wall; HWN, High Water Neaps; EHWS, Extreme High Water Springs. Picture taken at time of Low Water Springs and the new "Kom" had been emptied for cleaning. (Picture R. Dick)

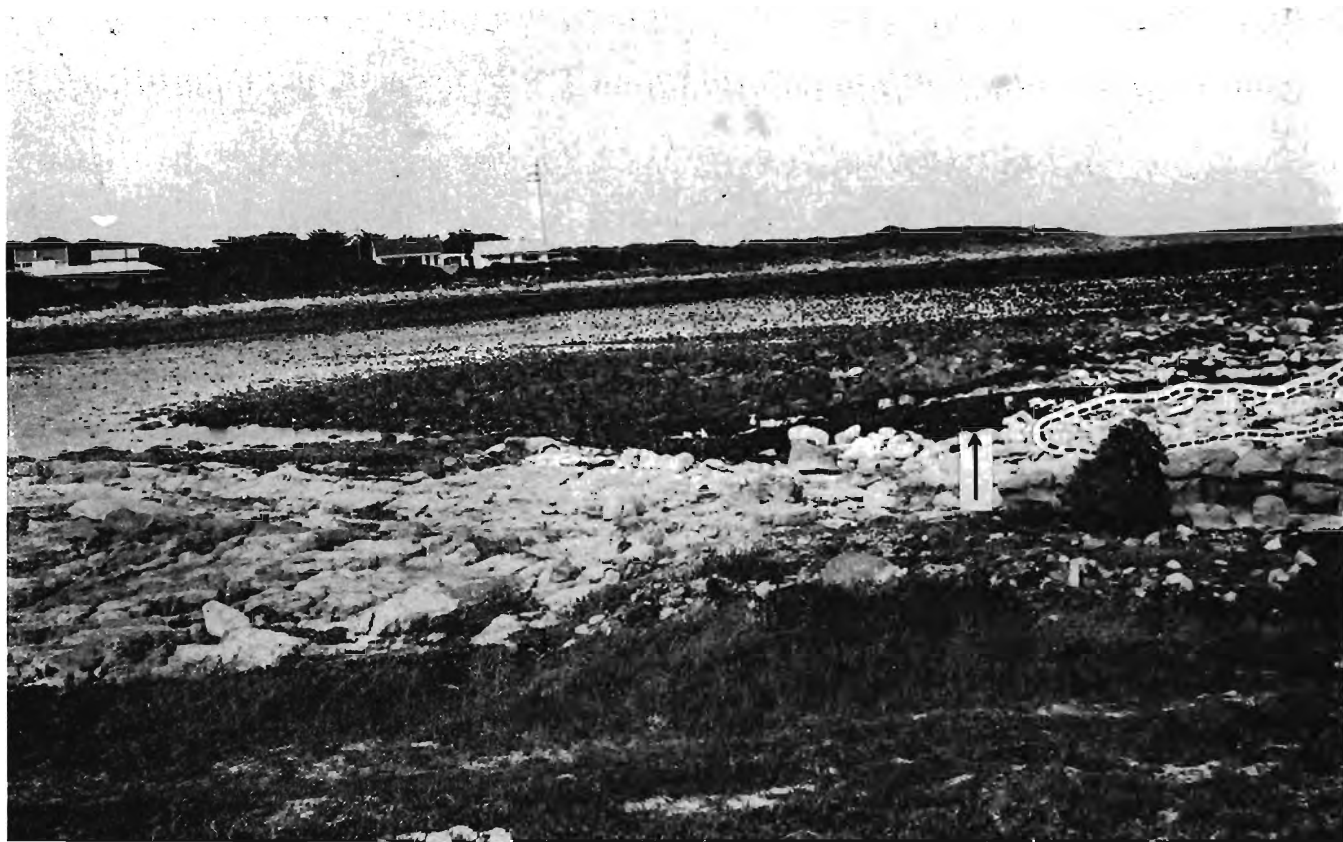


Fig. 6. Picture taken from above point c in fig. 2. The area shown is a bit larger than the area enclosed by points c, C, D in fig. 2. The Slangkop lighthouse is in the background. Picture taken at time of Low Water Springs. See text for explanation to the arrow and dotted line. (Picture R. Dick)



Fig. 7. Showing area approximately enclosed within points f, I, J, K of fig. 2. Note the darker rocks, i.e. a on picture, forming the narrow zone of the High Water Neaps belt, caused by the presence of *Calothrix crustata*. Also see text. (Picture R. Dick).

- (viii) Most of the infratidal fringe around "The Island" has a lot of kelp (see figs. 6 and 7) and there is no doubt that this contributes even further in breaking wave action and checking incoming waves.

IV PHYSICAL FACTORS AND THE DISTRIBUTION OF *D. FORMIDABILIS* AND *A. AFRICANUS*

(a) WAVE ACTION, TERRAIN AND THE NEST

D. formidabilis, *A. africanus* and *M. abrahami* use the same type of material and the same pattern in the construction and layout of their nests (see fig. 8 and 9). They mainly use the empty shells of *Patella*, *Amblychilepas*, *Crepidula*, *Diodora* and one valve of *Mytilus*, and occasionally use shells of *Oxystele* and *Burnupena* (Mollusca). It was found that they prefer limpet shells and this observation may be explained by the fact that this type of shell will remain more firmly wedged under rocks, in crevices and in gullies. Other types of shells were found to be easier to prize out from a wedged position and this would be a disadvantage to the spiders. They thus selectively choose a particular type of shell for their nest. They line the inside of the shell with silk (see fig. 9) closing it off completely before being submerged, trapping air within it, and they shear their way out at the thinnest part when the tide goes down.

It was observed that they modify their choice of shells according to the amount of wave action their nest will have to withstand at high tide. In exposed areas they inhabit shells that are firmly wedged in sheltered places such as gullies, rock crevices and under large rocks (see fig. 8 a and c). It is interesting to note that in this case the potential entrance to the nest nearly always faces downward so as to ensure that the air trapped in the shell during high tide will not escape so easily.

In areas where wave action is minimal at high tide, they even inhabit shells that are not wedged and merely rest on the rocks, (see fig. 8 b and fig. 9). This was found to be the case for:

- (i) *D. formidabilis* behind portions of the old "Kom" wall and amongst large rocks North of point f in fig. 2.
- (ii) *A. africanus* in area of high density between points C - d in fig. 3.

It was also found that *A. africanus* very often uses no shell at all and merely lines a crevice or the underside of a rock with silk (see fig. 8 d and fig. 10). The walls of such nests were found to be thicker in areas where exposures to wave action is greater, e.g. at western raised portions, than those of nests built in fairly sheltered areas such as between points C-d of fig. 3. Here again the potential entrance to the nest usually points or slants downwards.

Do these spiders use shells to protect their nests in other localities along the coast of the Cape Peninsula? The answer is yes and no. In areas where wave action is strong such as Blouberg Strand and Camps Bay, *D. formidabilis* and *M. abrahami* were mainly found in crevices between the tubes of *Gunnarea* (Polychaeta) and inside empty, but still firmly attached, barnacle plates. There may be two explanations for this, i.e. either the polychaete tubes and the barnacles form a more efficient protection against wave action, or the spiders use these as second best because there are only a few shells available as most empty shells

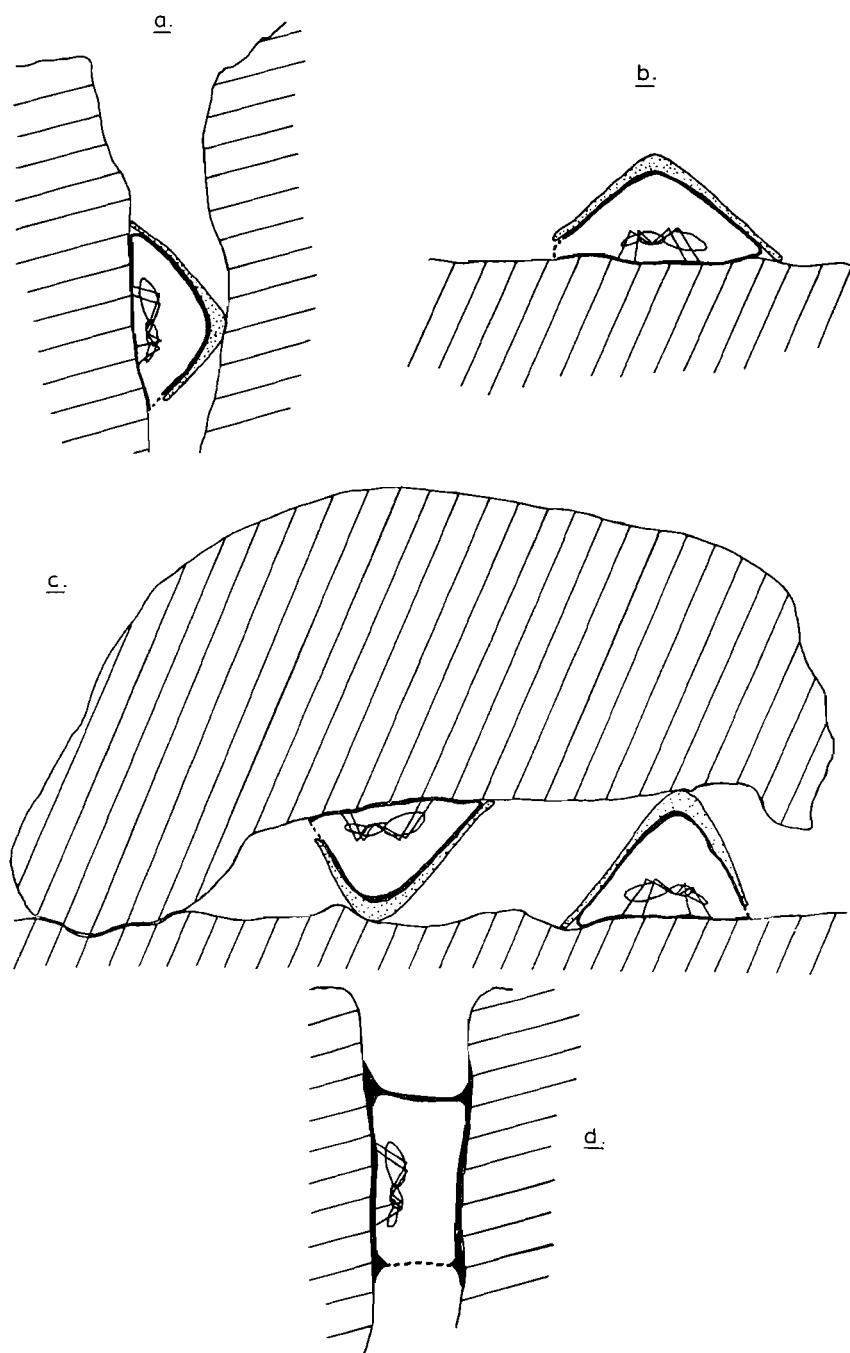


Fig. 8. a-d Showing various ways in which *D. formidabilis*, *A. africanus* and *Muizenbergia abrahami* build their nests. All drawings showing a longitudinal section through the nest.

//// = rock; :::: = limpet shell;

--- = site of entrance to nest.

— = thick silk lining of nest.

a. Shell wedged vertically in gully.

b. Shell not wedged but fastened to rocky substratum by silk.

c. Shells wedged horizontally under a rock.

d. No shell. Nest consists of thicker silk walls. Usually found in rock crevices.



Fig. 9. Showing an empty limpet shell used by *D. formidabilis* as nest. Note the thick silk walls on sides and bottom, securing the shell to the rock. (Picture R. Dick).

get shattered against the rocks by the strong wave action. *A. africanus* was found to be almost absent in such places.

On the other hand on more sheltered rocky shores such as St. James and parts of Pringle Bay, all three spiders were found. *D. formidabilis* and *M. abrahami* would use shells as well as polychaete tubes and empty barnacle plates for building their nests. *A. africanus* would use shells and rock crevices without shells.

E. littoralis, being such a small spider, will establish its nest in any part of its habitat that affords good protection. Any crevice will do. It was most often noticed to inhabit either occupied or empty *Desis* nests. It will suit the shape of its nest to the place it has chosen. When living in a nest occupied by *Desis* it was found not to build its own nest within it.

(b) IMMERSION AND ITS EFFECT ON RESPIRATION

Experiments were conducted on *D. formidabilis* and *A. africanus* to show that their air films (or air bubble of other authors) function as a physical gill when they are submerged. Resting respiration rates in air were determined for both to investigate any difference.



Fig. 10. Underside of a rock which was turned upside down to show nests of *A. africanus* in the region between points C and d on fig. 3. Portions of the nests were ripped off in the process, and two *A. africanus* can be seen in the remains of their nests (i.e. 5 and 7). Each number represents the position of a nest, illustrating the high density. The scale is life size. (Picture R. Dick).

Experiments were conducted to see whether air is absorbed from water, and in what quantities, for both spiders. These two experiments made it possible to study the comparative effectiveness of the air films. Dependence on the air films was tested by complete immersion of both types of spiders for a long period in well aerated sea water. This yielded survival times for both types.

Anatomical and histological investigations were also carried out to try and elucidate certain results obtained with the immersion experiment, and to find out whether any plastron is present.

The concept of a physical gill as postulated and proved by Ege (1915) for semi-aquatic insects is well known. It was thought that the air film of these spiders acts as a physical gill. Briefly, a physical gill operates in the following way. A spider with hydrofuge hairs will have a thin layer of air around its body when submerged. This layer will be in contact with the book lungs and the spiracles. If this layer were to serve merely as an air store, the spider would have to surface as soon as all the oxygen in that store is nearly used up; but these spiders can stay in well-aerated water for long periods. Thus the oxygen respired must be replaced.

Considering such a system, it has been shown in the case of semi-aquatic insects that oxygen diffuses across the boundary layer of the air film and surrounding water when the percentage of oxygen in the air film drops. Initially the composition of air in the air film is approximately 21 % O_2 , 78 % N_2 and 0.8 % CO_2 . The percentage of O_2 will drop as it is

being used up. The percentage of CO_2 will increase, but CO_2 produced will diffuse out almost instantaneously due to its high solubility in water. Its effect on percentage change is thus small. However, the air film will now contain a greater percentage of N_2 . To restore initial equilibrium, N_2 will tend to diffuse out into the water and O_2 from the water into the air film. Thus the animal will be able to renew its O_2 needs.

This situation is even bettered by the fact that, as Ege's work showed, the "invasion coefficient" of O_2 between water and air is almost three times greater than that of N_2 . Therefore, there will be a greater tendency for the air film equilibrium to be restored by diffusion of oxygen inwards than by diffusion of N_2 outwards. Theoretically, as most of the N_2 is retained, the air film should not decrease in size. But Ege showed that, as the CO_2 produced by the animal diffuses out much more rapidly than the O_2 diffuses in, a tension difference, affecting the N_2 composition will become established. Hence, some nitrogen

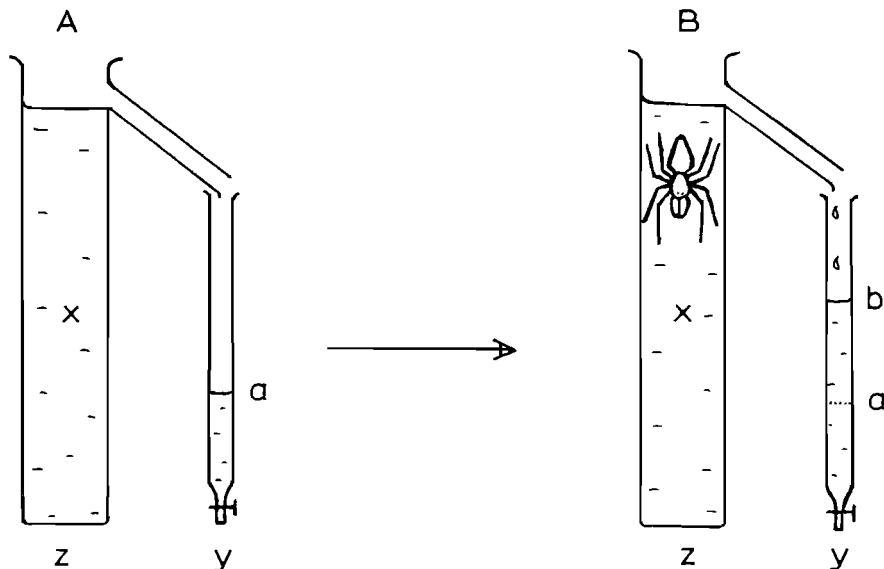


Fig. 11. Apparatus to measure body volume of spiders.

Order of procedure was A \longrightarrow B.

x = wetting agent solution; y = 2ml burette;

z = Narrow glass cylinder with side arm to direct overflow into burette.

a = initial reading of burette.

b = reading after spider is immersed. Therefore volume of spider = b-a. (Drawing not to scale).

will diffuse out of the air film and into the water—this factor was termed by Thorpe (1949 and 1950) the "Ege effect." The air film, due to this "Ege effect" will slowly decrease in volume and consequently in area until final collapse of the system.

Thorpe (1949, 1950) has pointed out that should there be a mechanical factor resisting this decrease of size of the air film, a terrestrial animal could live under water indefinitely, as it would in fact not have to surface in order to renew its air film. He found such a mechanical factor, namely strong short hairs, spaced at critical regular distances, on the

cuticle of *Aphelocheirus aestivalis*. He called the area covered by such hairs, a plastron, and suggested the term "plastron respiration" for insects using such a device. Plastron respiration is in fact by a physical gill that does not collapse.

If it can be proved that the concentration of O_2 in a known volume of water, not in contact with the atmosphere, and in which a spider is submerged, decreases, then a physical gill can be assumed to be in operation. This will be dealt with below.

(1) *Comparative effectiveness of air films.*

(i) Respiration in air:

Method and apparatus

The Warburg Constant Volume Respirometer as described by Umbreit Burris and Stauffer (1959) was used for this purpose. Briefly, the use of this apparatus depends on the principle that, in a system kept at constant temperature and volume, changes in the amount of gas present give rise to related pressure changes. Pressure changes are thus measured at known intervals and a formula (see Umbreit *et al* 1959) is used to convert this to a volume change.

A control was used, i.e. a manometer set up in exactly the same way as the others, but with no spider in it. Changes in readings of this control can only be caused by changes in temperature and atmospheric pressure, and it is thus adequately called a thermobarometer. This was used to correct each reading of the other respirometers.

Results obtained, after conversion, will be expressed in terms of μl oxygen consumed per milligram of wet body weight per hour at S.T.P. or QO_2 (w. wt.), following Umbreit *et al* (1959) conventions.

It was judged that dry weight reference was not essential, as this is not an experiment testing desiccation, and as there is very little chance of the spiders losing weight during the experiments. To level off conditions, all animals tested came from the same habitat and all were in good condition.

The CO_2 produced in respiration was absorbed with KOH placed in the centre well of the "normal" Warburg flask fitting onto the Manometer sidearm. Any pressure change observed after equilibrium of the apparatus is thus due purely to O_2 uptake. In order to have a constant temperature right through all experiments, these were performed in a constant temperature room where the t° was found to be $17^\circ C$, with a fluctuation not exceeding $0.5^\circ C$.

In the formula used to work out O_2 uptake of the animal, the volume of fluid and solid in the flask must be known. To work out the volume of the spiders, the apparatus and procedure described in fig. 11 was designed and built. A weak solution of a wetting agent prevented the formation of an air film and caused the spider to sink when dropped in the water. As the spider had been weighed before being immersed in the solution, the density of these spiders was worked out. This procedure was followed after having used the specimens for the Warburg readings.

Results

Whenever possible, the means of the results obtained in this investigation as a whole were analysed statistically.

TABLE 1

RESTING RESPIRATION RATES IN AIR OF *D. formidabilis* AND *A. africanus* WITH EXAMPLE OF STANDARD STATISTICAL ANALYSIS THEREOF.

Because all sample sizes tested are less than thirty and because the population variance σ_2 of QO_2 (w. wt.), is unknown, "student's" t-test is used. In each case an estimate of σ_2 is obtained.

	<i>D. formidabilis</i>		<i>A. africanus</i>	
	QO_2 (w. wt.) = x_1	x_1^2	QO_2 (w. wt.) = x_2	x_2^2
	.1121	.0126	.1426*	.0203
	.1216	.0148	.1154	.0133
	.0911	.0083	.0924	.0085
	.0798	.0064	.2385*	.0569
	.0934	.0087	.1936*	.0375
	.1168	.0136	.1159	.0134
	.1211	.0146	.1017	.0103
	.1654*	.0274	.1712*	.0293
Totals	$\Sigma x_1 = .9013$	$\Sigma x_1^2 = .1064$	$\Sigma x_2 = 1.1713$	$\Sigma x_2^2 = .1895$
Means \bar{x}	$\bar{x}_1 = .1127$		$\bar{x}_2 = .1464$	
\bar{x}^2	$\bar{x}_1^2 = .0127$		$\bar{x}_2^2 = .0214$	
Sample size	$n_1 = 8$		$n_2 = 8$	
$n\bar{x}^2$	$n_1\bar{x}_1^2 = .1016$		$n_2\bar{x}_2^2 = .1712$	

*indicates spiders that were observed to be slightly active, i.e. spinning or grooming.

Null hypothesis: $H_0: \mu_1 = \mu_2$ (i.e. equal population QO_2 (w. wt.) means.)

Alternative hypothesis: $H_a: \mu_1 < \mu_2$

Estimate of $\sigma^2 = S^2$

$$S^2 = \frac{1}{n_1 + n_2 - 2} (\Sigma x_1^2 - n_1 \bar{x}_1^2 + \Sigma x_2^2 - n_2 \bar{x}_2^2)$$

$$S^2 = \frac{1}{8+6} (.1064 - .1016 + .1895 - .1712) = .00165$$

$$S = .0406$$

number of degrees of freedom = 14.

$$t_{14} = \frac{|\bar{x}_1 - \bar{x}_2|}{S \sqrt{\frac{1}{n_1} + \frac{1}{n_2}}} = \frac{.1127 - .1464}{.0406 \sqrt{\frac{1}{8} + \frac{1}{8}}}$$

$$t_{14} = 1.66$$

From table of "t" (Hale, 1958) get $p = 0.5 - 0.1$. This is not significant, i.e. at a level of 50 — 90%. Therefore reject H_a and accept H_0 as the most likely hypothesis, i.e. the x_1 are not lower than the x_2 or QO_2 (w. wt.) of *D. formidabilis* is not lower than QO_2 (w. wt.) *A. africanus*.

The results of the resting respiration rate of *D. formidabilis* and *A. africanus* in air are presented in table 1. From analysis of means it may be inferred that an apparent sample mean difference is due to chance and does not reflect population mean. If p had been between 0.1 and 0.05 then the apparent significant difference in means would have required the use of the "comparison technique." This is not the case here. Furthermore, table 1 shows that seven out of eight *D. formidabilis* were truly resting compared to four out of eight for *A. africanus*. This will probably account for the apparent higher mean QO_2 (w. wt.) of *A. africanus*. Consequently it is inferred that:

QO_2 (w. wt.) *D. formidabilis* = QO_2 (w. wt.) *A. africanus* at rest.

A method was described in fig. 11 and text to show how the volume of these spiders was found. As they were weighed it was possible to work out their density. The corrected means were found to be:

D. formidabilis: 1.25

A. africanus: 1.03

(ii) Respiration in water

Method and apparatus

The method and apparatus used for this experiment is that described by Fox and Wingfield (1938) for the determination of oxygen dissolved in a small volume of water. Basically, the principle underlying the method used is that of Winkler for the determination of O_2 dissolved in water. As this method is often used to determine small changes in O_2 content of water samples it is referred to as the micro-Winkler method of Fox and Wingfield.

Fox and Wingfield (1938) used a small syringe which they called a syringe pipette to remove samples from water. The plunger movement is controlled by the number of turns of a long head screw that is fixed above it. Thus one complete turn of the head screw will only move the plunger a small fraction. The volume of the dead space in the nozzle of the syringe pipette, the volume of the barrel and the volume change caused by one turn of the head screw are calibrated before the experiment.

The syringe pipette is used to withdraw samples of water and test their oxygen content. The system from which the reading is taken must be shut off from the atmosphere or else O_2 will diffuse into the water to restore the equilibrium upset by the removal of O_2 from the water into the physical gill system. The syringe pipette also fulfils these requirements. It is therefore of the utmost importance that no air penetrates the syringe at any stage of the procedure as this will upset the readings. The whole analysis is carried out in the syringe, with the exception of the final titrations.

Fox and Wingfield (1938) used a constant flow apparatus to test the oxygen uptake of the animals they worked on. For the purpose of this investigation, where oxygen uptake from water for a small animal at rest is low, a different apparatus was designed and built.

The apparatus used is shown in fig. 12. The layer of paraffin at the top of the glass tube prevents oxygen diffusion into the water from air. A glass tube was used in order to present as little water surface as possible to the atmosphere. When about 2 cc. of sea water is withdrawn for sampling, the level in the glass tube will drop. The rubber stopper that fits tightly into the top of the plastic vial, can then be pushed down to bring the water level in the glass tube to its initial level. This must be done slowly or else the paraffin layer

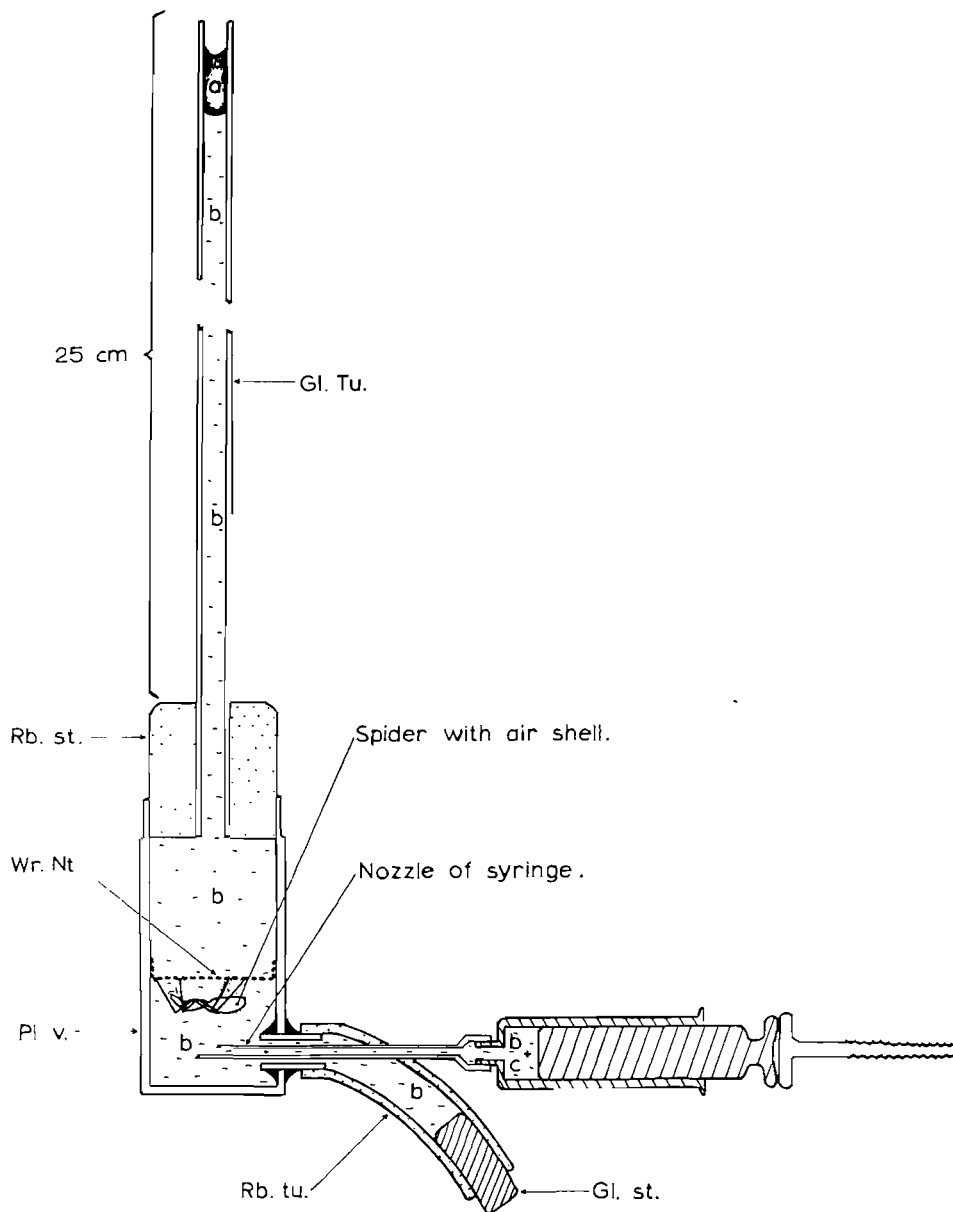


Fig. 12. Apparatus used to contain spiders during experiments measuring Oxygen uptake from water when immersed.

a = paraffin to prevent contact with air;
 b = Sea water; c = chemicals; Gl.Tu. = glass tube
 Rb.st. = rubber stopper; Wr.Nt. = wire netting;
 Pl.v. = plastic vial; Rb.tu. = rubber tube;
 Gl.st. = glass stopper stuck with glue to rubber tube.

will tend to stick to the glass and this may prevent it from successfully inhibiting O_2 diffusion into the sea water. To sample the water, the nozzle of the syringe pipette is pushed through the rubber tube at the bottom of the vial. On withdrawal of the nozzle the rubber will automatically seal the puncture site. The whole system is thus adequately air-tight for experimental purposes. Some O_2 may diffuse in after a few hours, but this would be irrelevant as by that time all readings required will have been taken. The water was sampled just before sealing the system and then again one hour later. The difference in reading will give us the amount of O_2 absorbed from the water by the spider using its physical gill. The results are then expressed as μl of O_2 absorbed from the water per hour, per mg. wet weight of spider at STP.

Fox and Wingfield (1938) express their results in ml. O_2 per litre water at STP using the following formula:

$$\text{Water Content} = \frac{0.028 \times \text{ml N/200 Na}_2\text{S}_2\text{O}_4 \text{ used} \times 1000}{\text{barrel volume of syringe in ml.}}$$

This formula was modified to be able to express the results in μl O_2 absorbed from the water per mg. wet weight, of spider, per hour at STP. The following procedure was adopted:

(i) Water O_2 content at start=

$$\frac{0.028 \times \mu l \text{ N/200 Na}_2\text{S}_2\text{O}_4 \text{ used} \times \mu l \text{ H}_2\text{O in closed system} \times 1000}{\text{barrel volume of syringe in } \mu l}$$

= x μl O_2 in vial at STP

(ii) Water O_2 content after 1 hour (using same formula)=

y μl O_2 in vial at STP.

\therefore vol O_2 absorbed from H_2O in vial = x — y μl O_2 /hour at STP.

\therefore vol O_2 absorbed by spider from H_2O in closed system per mg. wet weight per hour

$$= \frac{x - y}{\text{wt. of spider in mg.}} \mu l. O_2/\text{mg. wt./hr. at STP.}$$

We see that the results of O_2 uptake from water are expressed in the same units as QO_2 (w. wt.) in air with the Warburg respirometer. Accordingly the symbol QO_2 (w. wt. water, will be used when referring to O_2 uptake from water in this experiment.

To eliminate experimental error and allow comparison with the results obtained from the Warburg Constant Volume respirometer, all readings were taken under the same conditions, i.e. in the same constant temperature room at a temperature of 17°C . The water used in the experiment had first been equilibrated to this temperature for several days and well aerated prior to use. Finally, for each set of experiments, two controls were run concurrently and any change that occurred was subtracted from or added to the readings taken on vials containing spiders. Thus readings shown in table 2 have control corrections included.

It is realised that the QO_2 (w. wt.) water thus determined is not strictly speaking a true reflection of amounts taken up as we are using a closed system where O_2 tension in the water will drop after a while and so slow down diffusion across the interphase area of the

air film. But this experimental error will be the same right through and it can be neglected for our purposes as we are not measuring metabolic rates.

Results

As explained earlier QO_2 (w. wt.) water will be used to express the amount of O_2 taken up from water. The results and a statistical analysis of their means are represented in table 2, together with conclusive inference. In the course of experiments, once the reading

TABLE 2

QO_2 (W.WT.) WATER OF *D. formidabilis* AND *A. africanus* DETERMINED BY MICRO-WINKLER. RESULTS ANALYSED WITH "STUDENT'S" T-TEST.

	<i>D. formidabilis</i> QO_2 (w. wt.) water $= x_1$	<i>A. africanus</i> QO_2 (w. wt.) water $= x_2$
	.2340	.1483
	.2033	.2691
	.1611	.0954
	.1724	.2837
	.2135	.2056
	.2840	.2453
	.1950	.1850
	.1834	.1929
	$\Sigma x_1 = 1.6467$	$\Sigma x_2 = 1.6253$
Means	$\bar{x}_1 = .2058$	$\bar{x}_2 = .2032$
Sample size	$n_1 = 8$	$n_2 = 8$

Null hypothesis: $H_0: \mu_1 = \mu_2$ (equal sample means)

Alternative hypothesis: $H_a: \mu_1 > \mu_2$

$S = .0513$; $t_{14} = .1015$

From table of "t" (Hale, 1958) get $p \gg 0.5$.

Therefore H_a is rejected and H_0 accepted, i.e. at a level greater than 50%

Thus under equal experimental conditions the physical gill of *A. africanus* is just as efficient as that of *D. formidabilis* in taking up O_2 from water.

of *D. formidabilis* had been converted, 5 blank readings after one hour were also converted to QO_2 (w. wt.) water. The means of blanks were tested against the means of 5 animals, using a "t" test, to see if the results obtained with the micro-Winkler were significant of O_2 uptake. $H_0: \mu \text{ blanks} = \mu \text{ spiders}$, $H_a: \mu b < \mu s$. t_8 was found to be equal to 8.55. Thus get $p < 0.001$ from table of "t" (Hale 1958). This is highly significant and thus reject H_0 and accept H_a , i.e. we can say that the readings obtained show actual O_2 uptake from water.

(2) Dependence on air film.

Method and Apparatus

The aim of this experiment was to observe the effects of prolonged immersion on *D. formidabilis* and *A. africanus* when placed in well-aerated water. Twenty *D. formidabilis* and twenty *A. africanus* were placed in little cages built from plastic mosquito-net. These were then attached linearly with rubber bands to 4 long and narrow glass panes. The glass

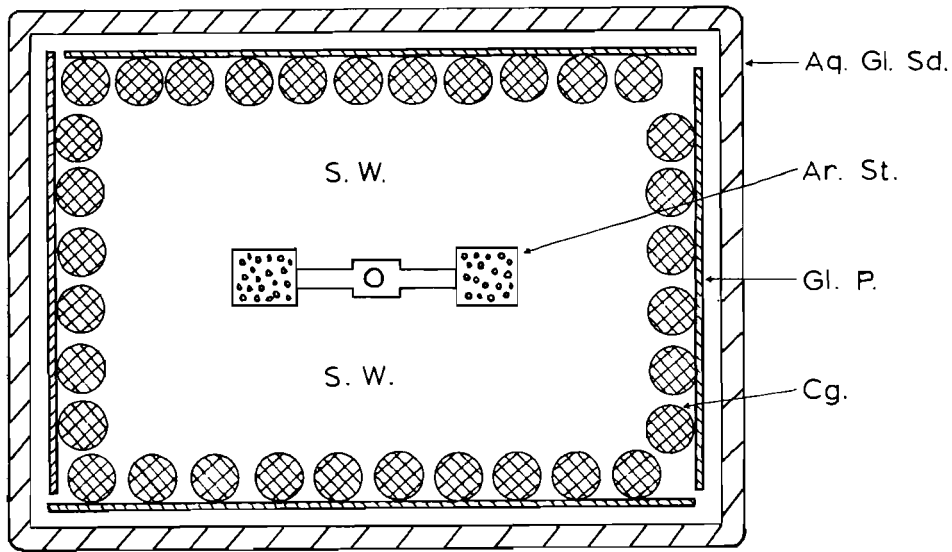


Fig. 13. Diagrammatic representation showing the aquarium, as viewed from the top, used in prolonged immersion experiment.

Aq.Gl.Sd.=aquarium glass side; Ar.St.=air stone; Gl.P.=glass pane; Cg.=cage; S.W.=sea water.

panes were then lowered in an aquarium filled with sea water and each held parallel to one of the sides of the aquarium by means of wire hooks. Each cage and its contents could thus be observed carefully through the side panels of the aquarium. The air supply was delivered through two porous stones placed in the centre of the aquarium to provide ample aeration together with good circulation of the water, (see fig. 13). The air bubbles emanating from the porous air stones were not allowed to drift into the plastic cages.

Here again the experiment was performed under constant temperature, i.e. 17°C. When the water temperature rose due to aeration, a small polythene bag containing ice blocks was lowered in the centre of the aquarium until the temperature was back to 17°C.

Results

The results obtained are presented in table 3. From these it seems that although *D. formidabilis* tends to lose its air bubble earlier than *A. africanus*, in the end the former has resisted prolonged immersion better, as borne out by the number of specimens that survived. This cannot however be taken as a final conclusion and further investigation might be required to substantiate such a conclusion.

It is interesting however, to note that both can survive for more than 12 hours after the loss of their physical gill.

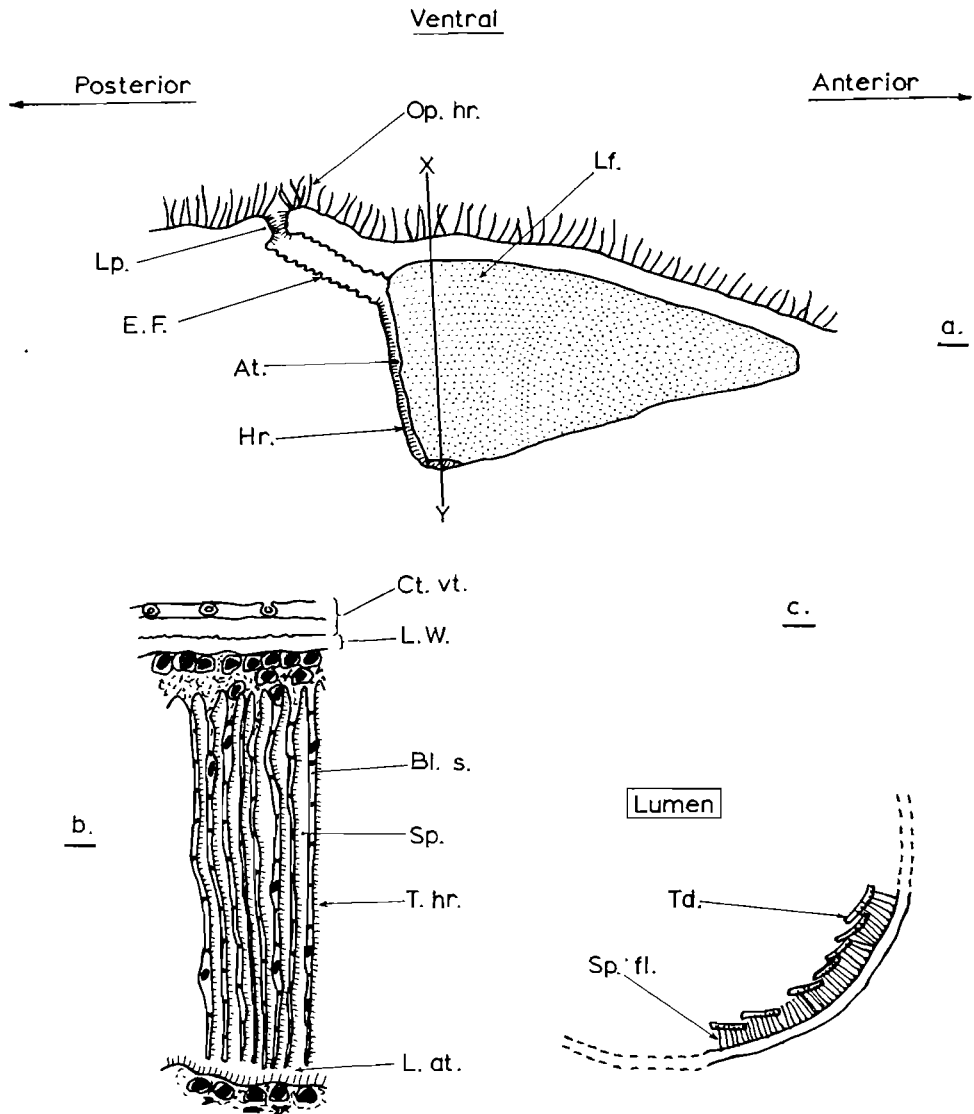


Fig. 14. a-c. Various aspects of the respiratory system of *D. formidabilis*.

a. Diagrammatic representation of a sagittal section through one of the booklungs.

b. Transverse section through the booklung along X-Y of diagram a., to show structure of leaves.
(Drawn under H.P.)

c. Transverse section through a trachea. Drawing showing only part of the tracheal wall.

At. = atrium; Bl.s. = blood sinus; Ct.vt. = ventral cuticular layers;

E.F. = glabrous epigastric furrow; Hr. = small hairs facing the leaves of the booklungs; L.at. = lower part of atrium; Lf. = "leaf" with its plane in that of the page, small dots represent tiny hairs; Lp. = "lip" with dense small hairs; L.W. = lung wall;

Op.hr. = opisthosomal hydrofuge hair; Sp. = space between leaves;

Sp. fl. = supporting filaments; Td. = taenidium; T.hr. = tiny hairs.

TABLE 3
RESULTS OF PROLONGED IMMERSION EXPERIMENT

Events	<i>D. formidabilis</i>		<i>A. africanus</i>	
	No. of individuals	Time after start of experiment (in hours)	No. of individuals	Time after start of experiment (in hours)
Air film collapse	1	8	1	8
	10	8½	2	9
	1	9	5	10
	6	11½	9	10½
	2	12	2	11
			1	11½
Air film lost but well alive	20	12	20	11½
Lethargic	10	17	10	13
	16	19	14	15
	20	21	17	17
	20	23	20	19
	20	24	20	24
Removed from Water	20	24	20	24
Slightly active to motionless but alive	17	24½	12	24½
Apparently dead	3	24½	8	24½
Recuperated completely after exposure to air	20	34	14	34
Established dead	0	40	6	40

(3) *Anatomical and histological investigations relating to the above results.*

Methods

Female specimens of *D. formidabilis* and *A. africanus* were examined externally under a dissecting microscope to find any signs of a plastron near the booklung opening or spiracular opening. Areas of the cuticle on the body and around the openings to the respiratory organs were also mounted in glycerol on a slide and examined under the compound microscope. Whole booklungs and portions of the spiracle and trachea were also treated in order to cut sections. The material was fixed in Bouin, cleared in Methyl Benzoate celloidin and embedded in ceresin wax. 10 μ sections were then cut and mounted on slides. The sections were then stained in Mann's Methyl Blue-Eosin (Pantin 1964).

Results

Figs. 14 a-c represent certain aspects of the respiratory system of *D. formidabilis*. No marked differences were found for the same structures in *A. africanus*, and this figure thus also applies to it.

No plastron was found to occur on any external surface of both spiders. It was however noticed that the density of hairs is greater on the "lips" of the slits leading to the booklungs of these spiders. These hairs were found to be shorter than those on the ventral surface of the opisthosoma. The epigastric furrow was found to have no hairs at all but the wall facing the "leaves" of the booklungs beyond the epigastric furrow was covered with small hairs placed at fairly regular intervals, (see fig. 14a).

Transverse sections of these booklung leaves showed them to have tiny hairs or projections at regular intervals (see fig. 14b). Millot (1949) says they are chitinous. Millot describes them thus: "De petites tigelles de chitine, issues de la cuticule supérieure des lamelles, maintiennent celles-ci écartées, les unes des autres et permettent entre elles une constante circulation d'air." They thus facilitate air circulation by preventing the leaves from adhering to each other.

Richards and Korda (1950) report that the presence of taenidia in the tracheae of araneids is not the general rule. Barnes (1966) says they occur but he does not state how frequently. Fig. 14c shows that taenidia together with supporting filaments are present in both these spiders. The taenidia form helices that run along the length of the trachea and tracheoles. Thus when cutting transverse sections only bits of taenidia are observed.

Both types of spiders were found to have a small atrium beyond the spiracles. The spiracular opening also has small hairs similar to those on the "lips" of the book-lungslits, but the atrium has none. Beyond this no hairs were found.

(c) DESICCATION

Desiccation tests were carried out to find whether there is any appreciable difference in the rate of water loss between *D. formidabilis* and *A. africanus*.

Method and apparatus

The apparatus used is an ordinary desiccator with Calcium chloride granules at the bottom. For all practical purposes, CaCl_2 can be taken as resulting in a relative humidity (R.H.) of 0%. The cages built for the prolonged immersion experiment were used to enclose the spiders, ensuring that they were well dry. The spiders were put in the desiccator for 3 hours with the lid well closed and sealed off with vaseline. They were then weighed accurately and left in the desiccator for a further 12 hours. At the end of this time they were withdrawn from the desiccator individually and again weighed. The amount of water loss by desiccation was calculated as the % loss of H_2O per hour per original body weight.

Results

Results are presented in table 4. Statistical analysis shows that there is no significant difference in the rate of water loss at 17°C for these two spiders. The implications of this will be discussed further.

TABLE 4

RESULTS OF DESICCATION TEST ON LIVE *D. formidabilis* and *A. africanus*.
MEANS TESTED BY "STUDENT'S" T-TEST.

	<i>D. formidabilis</i> % loss/hr. = x_1	<i>A. africanus</i> % loss/hr. = x_2
	.351	.203
	.431	.343
	.041	.209
	.595	.037
	.614	.320
	.897	.030
	.488	.250
	.450	.100
	.726	.142
	.416	.146
	.461	.226
	.918	.150
	.066	.218
	.351	.213
	.447	.382
Totals	$\Sigma x_1 = 7.252$	$\Sigma x_2 = 2.969$
Means	$\bar{x}_1 = .483$	$\bar{x}_2 = .198$
Sample sizes	$n_1 = 15$	$n_2 = 15$

Null hypothesis: $H_0: \mu_1 = \mu_2$ (equal pop. means)

Alternative hypothesis: $H_a: \mu_1 > \mu_2$

$$t_{28} = 0.39$$

From table of "t" (Hale 1958) get $p > .5$.

Therefore H_a rejected and H_0 accepted, i.e. at a level greater than 50%. Thus under equal experimental conditions of desiccation there is no significant difference between the rate of water loss, by evaporation, of these two spiders.

(d) TEMPERATURE

No experiments to test the effect of temperature were carried out on *D. formidabilis* and *A. africanus* due to time limitations imposed on this investigation. However, the following observations were recorded:

- (i) An equal number of both spiders kept in small cages, exposed to air (never submerged) in the constant temperature room at a temperature of 17°C and R.H. of 85%, survived well for a period of seven days.
- (ii) If the same batches of spiders were kept in the same cages and exposed to air (never submerged) where temperature fluctuation was 18° - 28°C and R.H. 75 - 85%, it was noticed that half of the *D. formidabilis* but none of the *A. africanus* were dead after seven days.

V BEHAVIOURAL ADAPTATIONS TO
PHYSICAL FACTORS

(a) HUNTING BY NIGHT (DIURNAL RHYTHM)

All four species were found to be mainly active at night. No spiders were even seen running about or catching prey (except for animals that tried to get into their nests) during daytime. This was observed both at "The Island" and on laboratory animals. They simply remain in their nests right through the day whether they are covered by the tide or not. They were also found to be less active when covered by the tide during daytime, this probably in order to conserve the air reserve in their nests which, incidentally, can last them for several days. As soon as darkness has appeared they become more active if the tide is low. They catch prey in two different ways. They either only emerge partly from their nests, pouncing on potential prey that passes by, or they leave their nests to go in search of prey. If the tide is high they usually stay in their nests at night. They were never seen to catch prey under those circumstances. However, the fact that they were never seen to catch prey when submerged even when out of their nests does not mean that they cannot do so.

(b) SPINNING IN TIDAL RHYTHM

It was interesting to note that *D. formidabilis* and *A. africanus* seem to have a built-in mechanism which regulates their activity with tidal rhythms. This was found to be more pronounced with the former. It was noted that spiders caught at the beginning of a collecting trip, when the tide was still low, would remain fairly passive in their vials until the time when the tide would rise. At such times they would start to line the vials in which they were, with silk walls, this presumably to build a shelter against the rising waters. Spiders caught when the tide was rising would start spinning a nest as soon as they were in the vials. Testing (at night) spiders newly settled in the aquaria, with the water level down, it was found that if their nests were destroyed at a time when the tide would start to go down on the shore, they would not bother to find a new nest or build a new shelter until such time as the tide would normally start to turn on the shore. Those whose nests were destroyed at the latter time, immediately started to seek a new shell or spin a silk nest in a crevice. This behaviour, however, did not last longer than a week after which time they adapted themselves to the artificial tides of the aquarium.

VI BIOTIC FACTORS INFLUENCING THE DISTRIBUTION
OF *D. FORMIDABILIS* AND *A. AFRICANUS*

(a) ASSOCIATED FAUNAS

Some interesting relationships between these spiders and other invertebrates, besides those they prey on, were found.

It was hoped at the beginning of this investigation to be able to establish the diet of these spiders by identifying remnants of prey. No such remnants could however be found. Subsequently it was discovered that the Collembolan, *Anurida maritima*, scavenges the nests of *D. formidabilis* and *A. africanus*. They do this as soon as the spiders have finished with their prey. *Anurida maritima* is not only found in the nests of *D. formidabilis* and

A. africanus. They are general scavengers of the intertidal zone, and are always present in nests where prey has been discarded by the spiders. *A. maritima* is velvety and steel-grey to blue-grey in colour; it reaches a maximal length of 3 mm. It is also found floating in vast numbers in tidal pools. If submerged it will have an air film around its body. When plunged in 70% alcohol, it will not be wetted at all for 2 to 3 days.

A small Hymenopteran (approximately 1.5 mm. in length) belonging to the family Scelionidae was found parasitising the eggs of *D. formidabilis*. Dr. L. Masner (Institute of Entomology, Czechoslovak Academy of Sciences) kindly agreed to identify the material and found it to represent a new genus and species, which he has described as *Echthrodesis*

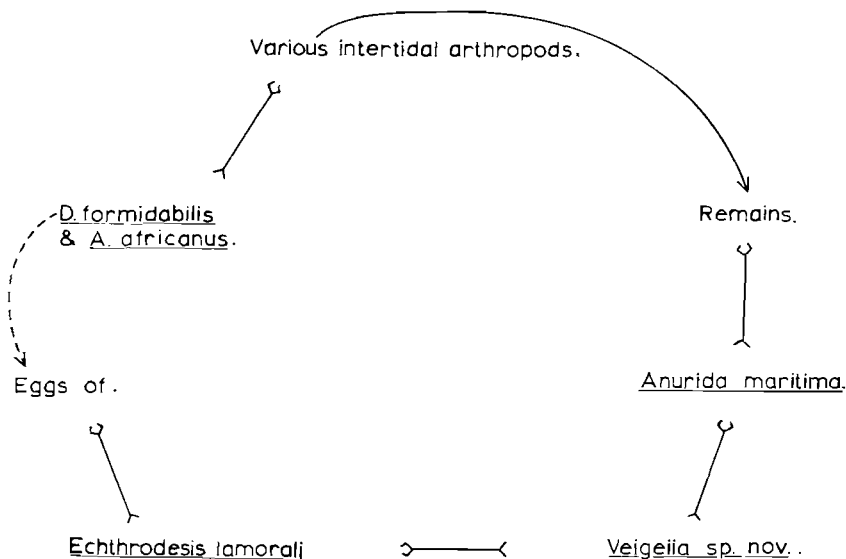


Fig. 15. Diagrammatic representation of relationships between intertidal invertebrates directly or indirectly associated with *D. formidabilis* and *A. africanus*. Symbols: (1) $\text{---} \text{C}$ indicates predator-prey relationship, i.e. predator $\text{---} \text{C}$ prey. (2) $\text{---} \text{>}$ indicates ultimate result of such predation. (3) $\text{---} \text{>}$ indicates aspect that is affected by predation or parasitism.

lamorali in this issue of the *Annals of the Natal Museum*. According to Masner (1968), this is "the very first evidence of an intertidal maritime scelionid ever known." These Scelionid wasps were found in and around nests of *D. formidabilis*. Dense pilosity combined with marked apterism clearly suggest an adaption of the parasite to the intertidal habitat of its host. The wasp was found only in association with the nests of *D. formidabilis* and in none of these of the three other spiders studied. This suggests that *Echthrodesis lamorali* is monophagous.

Finally a new species of mite was found in and around the nests of *D. formadabilis* and *A. africanus*. Specimens were sent to Dr. G. C. Loots of the Institute for Zoological Research, at Potchefstroom, who kindly identified them as follows:

Subclass	Acari
Order	Mesostigmata
Superfamily	Gamasina
Family	Veigeiidae
Genus	<i>Veigeia</i>
Species	sp. nov.

Dr. Loots has informed me that he will describe the new species in the course of 1968.

Veigeia sp.n. was found to be a predator on *Echthrodesis lamoralis* and *Anurida maritima*. The relationships between these various invertebrates has been represented diagrammatically in fig. 15.

(b) PREY PREFERENCES OF *D. formidabilis* AND *A. africanus*

As explained above, no inference on the diet of these spiders was possible from prey remains as none were found.

TABLE 5
LIST OF VARIOUS ANIMALS THAT *D. formidabilis* AND *A. africanus*
ACCEPTED OR REFUSED AS PREY

Prey	<i>D. formidabilis</i>	<i>A. africanus</i>
<i>Paridotea</i> spp. (isopoda)	+	—
<i>Exospheroma laeviusculum</i> (isopoda)	+	—
<i>Parisocladius stimpsoni</i> (isopoda)	+	—
<i>Hyale</i> spp. (Amphipoda)	+	—
<i>Ligia dilatata</i> (isopoda)	—	+
<i>Talorchestia capensis</i> (amphipoda)	—	+
<i>Deto echinata</i> (isopoda)	—	+
<i>Telmatogeton minor</i> (Diptera)	+	+
<i>Pycnogonida</i>	+	—
<i>D. formidabilis</i>	—	+
		(juveniles)
<i>A. africanus</i>	+	—
<i>Palaemon pacificus</i> (Decapoda)	—	—
Other decapoda	—	—
Polychaeta	—	—
Mollusca	—	—
Pisces (small)	—	—

+ = killed and eaten

— = not caught, or if killed, then not eaten.

Table 5 provides a list of the intertidal arthropods these spiders fed on or rejected. This list was deduced from observations of actual prey catching at "The Island" (few) and in the laboratory (most) at night, by supplying them with various potential prey. This does not imply by any means that these are the only intertidal invertebrates these spiders feed on. It is merely a list of the animals they were seen feeding on.

The first thing that strikes one is that *D. formidabilis* does not feed on animals that *A. africanus* feeds on and *vice versa*. Is this due to the fact that in natural conditions the

spiders do not do so because certain prey owing to its zonation does not occur in certain intertidal regions, or is it because these spiders have become selective of their prey?

Experiments were conducted in the laboratory to test prey preference. A mixed batch of prey, comprising on the one hand ten individuals of three different types of animals that *D. formidabilis* normally feeds on, and on the other hand ten individuals of three different types that *A. africanus* normally feeds on, was placed in the aquarium containing approximately 25 *D. formidabilis*, at the end of a day. An identical batch of prey was placed in the other aquarium containing approximately 25 *A. africanus*, at the same time.

The spiders in both aquaria had not been fed for a week. On the following morning a census of the remaining prey was taken. The results are presented in table 6. It seems,

TABLE 6

RESULTS OF EXPERIMENT TO TEST PREY PREFERENCE OF *D. formidabilis* and *A. africanus*.
(see text for explanations)

Prey	<i>D. formidabilis</i> aquarium		<i>A. africanus</i> aquarium	
	No. of prey before experiment	No. of prey after experiment	No. of prey before experiment	No. of prey after experiment
<i>Paridotea</i> spp.	10	4	10	10
<i>Parisocladius stimpsoni</i>	10	7	10	9
<i>Exospheroma laevisculum</i>	10	5	10	9
<i>Ligia dilarata</i> (juveniles)	10	10	10	3
<i>Talorchestia capensis</i>	10	9	10	6
<i>Deto echinata</i>	10	10	10	5

therefore, that the spiders are selective of their prey. Although this experiment is indicative of the fact that they have a selective diet this can by no means be a conclusive statement. More experiments of this kind would be necessary and factors such as a greater knowledge of which other animals, besides those in table 5, they catch, would be necessary. The whole investigation would also require statistical analysis.

(c) INTRASPECIFIC COMPETITION FOR NESTING SITES IN *D. formidabilis* AND *A. africanus*

(1) *D. formidabilis*

It can be seen from fig. 2 that there are areas of great concentrations of these spiders. This raises the questions as to whether there is a critical number of individuals per unit surface area. Do they prey on each other as many araneids do?

It was found that in the aquarium (4,000 cm.²), there was a critical number per surface area. If there were more than 30 spiders in the aquarium they would start to attack each other until their numbers were reduced to the level of 30. It was then wondered whether this might not be due to the fact that there were only enough shells or crevices to house about 30 spiders and not because the spiders would not allow other spiders, of the same species, to settle within a certain periphery of their nest.

Thirty potential nest-building sites (shells and cracks in rocks) were counted in the aquarium. The answer to the above question was provided by adding more shells to the same aquarium (therefore the same area), giving a total of 50 potential nest-building sites, certain shells being placed next to each other. Forty freshly collected specimens were then added to the aquarium and counts taken on the following and subsequent days. The aquarium housed about 57 spiders on the following day and 13 had been killed and eaten as shown by bits of their limbs floating on the water. Once the population was down to 55-57, very few spiders were found missing and those that died on subsequent days died from causes other than cannibalism as their bodies were recovered intact. Shells that were placed next to each other all contained spiders and they did not attack each other. From these results it is logical to conclude that the density of a population for a certain area depends entirely on the availability of shelter or the number of potential nesting sites and not on a critical number of individuals for that area.

When new spiders were put in the aquarium, they were seen to go immediately in search of a shelter. In doing this they would quite often try to slip under a shell that already contained a spider. If the resident spider was bigger, the intruder would not insist. If the resident spider was smaller, the intruder would evict it and take possession of its nest, provided the shell was big enough for the intruder. The smaller spider would, in that case, not insist too much on defending its nest, slip out, unharmed most of the time, and start looking for a new shell. When most shells had been occupied spiders that could not find a nesting site would become bolder and try to evict even bigger spiders. If the two contenders to a nest were females, one was invariably killed. If one of the two was a mature male, the intruder would be allowed to share the nest. It was interesting to note that in about 50% of the cases, two males, whether mature or not, would peacefully share the same nest.

To summarize, females as a rule will not share a nest with another female; mature males and females will share a nest and males seem to be more tolerant towards their own sex.

When hunting at night, two individuals may start fighting when coming across each other, but the smaller one usually quickly breaks off to run away to safety and the bigger one does not pursue it.

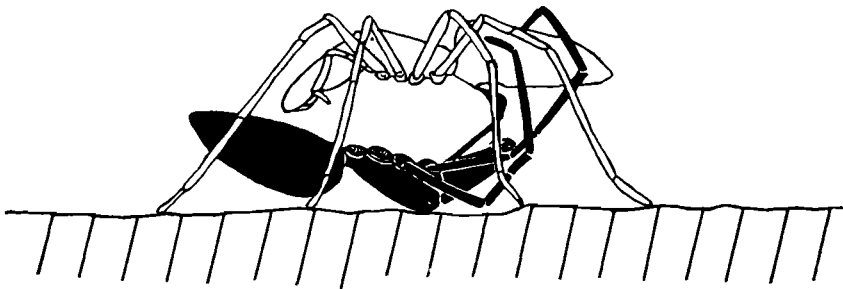


Fig. 16. Mating of *D. formidabilis* seen in lateral view. Male in black. Male pedipalp is seen behind third leg of female. Legs 3 and 4 of male omitted to prevent confusion in drawing. Leg 3 of male is normally wrapped round anterior part of female's opisthosoma and leg 4 round the prosoma passing between leg 2 and 3 of female

These observations lead to the conclusion that these spiders show a certain amount of colonising behaviour, provided there are enough potential nest sites available. This was also found to occur in their natural habitat at "The Island." Hence density and a certain amount of colonising behaviour are controlled mainly by the availability of shelters.

Matings of *D. formidabilis* were observed in many instances; males and females were observed to adopt the position sketched in fig. 16. A male living with a female in a shell does not go through an elaborate courtship pattern, and merely starts tapping the female's epigyne with its pedipalps to test female preparedness. If the female is ready she will allow the male to start copulation. If not she will merely brush him away.

(2) *A. africanus*

It was found that the density of a population in a given area is also regulated by the availability of prospective shelter and not by a critical number of individuals per unit surface area. *A. africanus* shows even greater population density than *D. formidabilis* in sheltered areas. Figure 10 illustrates this very well. Ten spiders were found established on a surface of 100 cm.². On the other hand these spiders do not seem to share their nests with their kin quite as easily as *D. formidabilis*. Males were never found in females nests and instead had their own nest next to that of a female. Copulation was never observed and thus cannot be described.

Both *D. formidabilis* and *A. africanus* keep their young with them in their nests once these have hatched. The young remain until after the first or second moult. In *A. africanus* the mother dies soon after the young have left. This was not found to be the case with *D. formidabilis*.

D. formidabilis, *A. africanus* and *M. abrahami* were never seen to build any web and their serigenous activity is mainly concerned with lining their nests, egg cases and producing a dragline when moving about. *E. litoralis*, being an Argiopid, might be expected to build an orb web, but this was not observed. Knowledge of this spider's activities being rather scanty, it would not be logical to conclude, however, that it does not build a web.

(d) INTERSPECIFIC COMPETITION BETWEEN *D. formidabilis* AND *A. africanus* FOR

NESTING SITES

When these two species are placed together, *D. formidabilis* invariably gets the upper hand over an *A. africanus* of the same or even slightly bigger size. Large *A. africanus* can overcome *D. formidabilis* half their size. Should *D. formidabilis* invade the territory of *A. africanus*, it can be expected that the former could well eradicate the latter. This was repeatedly tested in aquaria. When equal numbers of spiders in equal proportions of size for each species were put in the same aquarium, *D. formidabilis* was *always* the sole survivor. What gives *D. formidabilis* this superiority? It is suggested that this is due to the relatively much larger size of its chelicerae. Fig. 17 shows that, in two specimens of the same body size, the chelicerae of *D. formidabilis* are much larger and longer, *D. formidabilis* has its chelicerae three times the length of its opponent's when fully extended. Furthermore, the chelicerae of *D. formidabilis* operate in almost the same axis as the antero-posterior axis of its body, giving them a greater forward reach. *A. africanus* has its chelicerae operating

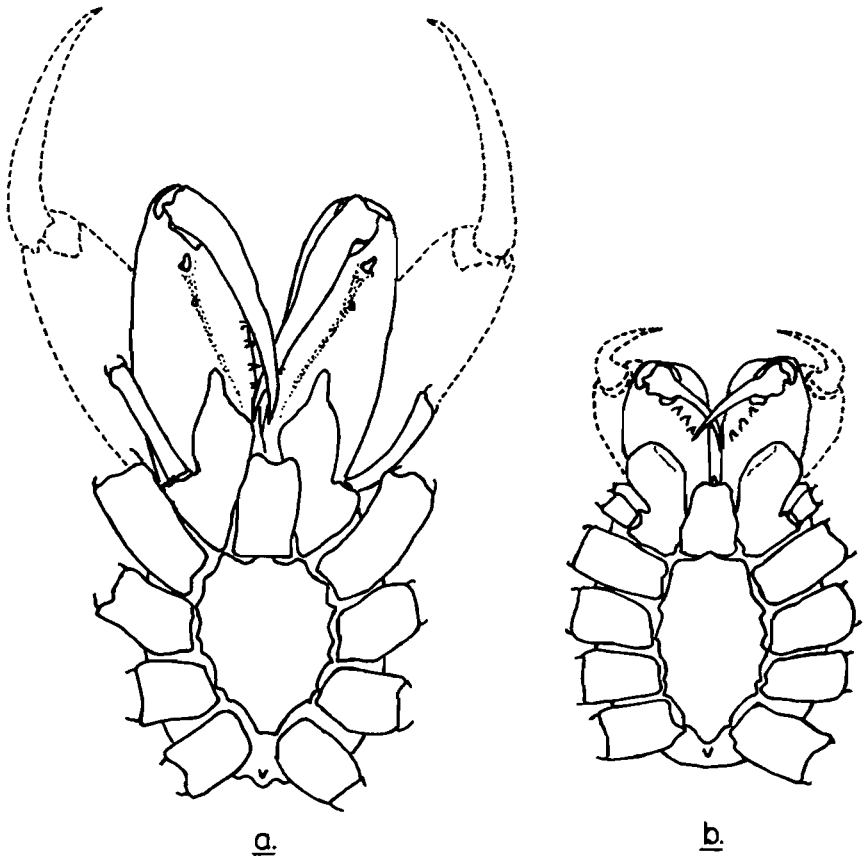


Fig. 17. Ventral view of the prosoma of: *a*, *D. formidabilis* (♀) and *b*, *A. africanus* (♀) of equal body lengths to show the difference in size of their chelicerae. The dotted outline shows the position of the fangs and basal segments of the chelicerae when these are opened for biting. Legs and pedipalps, except their coxae, omitted.

in an axis perpendicular to the antero-posterior axis of its body, thus not improving their forward reach.

Bearing the above in mind one is faced with the following situation: *A. africanus* cannot invade *D. formidabilis*' territory as it would be driven out or killed and thus it has to remain in its own territory. We are, therefore, left with the problem of finding what prevents *D. formidabilis* from invading *A. africanus*' territory. A criticism that could be levelled to this approach is that spiders do not invade other spiders territory and eradicate them. This may be true for terrestrial spiders where territories are vast, offering an almost unlimited number of diversified habitats and prospective nest sites. The situation in the intertidal zone is however quite different. Prospective nest sites are limited as was shown above. There are only a few alternatives (i.e. shells, rock crevices, polychaete tubes, barnacle plates and a few others), and these are made use of by both *D. formidabilis* and *A. africanus*.

As was shown earlier, there is an intraspecific competition for nest sites when these are limited, this being a factor limiting the small amount of colonising behaviour observed. There is however no colonising behaviour on the interspecific level and competition for nest sites becomes acute. This is supported by the very fact that zonation of nest sites as shown in figs. 2 a and b is very sharp.

VII DISCUSSION AND CONCLUSIONS

It is now possible to assess the effects of the factors investigated above on distribution and zonation.

(a) THE ROLE OF PHYSICAL FACTORS

(1) Wave action

D. formidabilis and *A. africanus* have been shown to modify their choice of shells according to the amount of wave action their nest will have to withstand. Wave action has been shown to be an important factor in the distribution and density of all species investigated. It can also be concluded that wave action does not selectively favour any species with regard to zonation and that all species are equally well adapted to this factor.

(2) The air film or air bubble

(i) Mechanism and comparative effectiveness of the air film of *D. formidabilis* and *A. africanus*.

The mechanism of a physical gill and factors required for its function have been described under IV (b). To prove that the air bubble or air film of these spiders functions as a physical gill, one does not need to go through all the experiments attempted by other workers on the air bubble of aquatic Hemiptera. It is not difficult to understand that, provided we can prove that these spiders actually absorb O_2 from water using their air film, a physical gill is in operation. This was successfully proved by the use of the micro-

TABLE 7
TO COMPARE MEANS OF QO_2 (w. wt.) AIR WITH QO_2 (w. wt.) WATER OF *D. formidabilis* and *A. africanus*.
STATISTICAL ANALYSIS THEREOF, USING "STUDENT'S" T-TEST. MEAN QO_2 (w. wt.)
FROM TABLE 3 AND MEAN QO_2 (w. wt.) WATER FROM TABLE 4.

<i>D. formidabilis</i>		<i>A. africanus</i>	
QO_2 (w. wt.) = x	QO_2 (w. wt.) water = x_2	QO_2 (w. wt.) = x_3	QO_2 (w. wt.) water = x_4
$\bar{x}_1 = .1127$ $n_1 = 8$	$\bar{x}_2 = .2058$ $n_2 = 8$	$\bar{x}_3 = .1464$ $n_3 = 8$	$\bar{x}_4 = .2032$ $n_4 = 8$
$H_0 = \mu_1 = \mu_2$ $H_a = \mu_1 < \mu_2$ $t_{11} = 5.855$ $p < 0.001$		$H_0 : \mu_3 = \mu_4$ $H_a : \mu_3 < \mu_4$ $t_{14} = 1.986$ $p = 0.1 - 0.05$	
This is highly significant i.e. at level $>99.9\%$ therefore reject H_0 and accept H_a ; i.e. QO_2 (w. wt.) water is greater than QO_2 (w. wt.) air.		This is significant but not highly and further test would be required. Level of significance = 90-95%.	

See discussion for possible explanation of above results.

Winkler method as demonstrated by the results in table 2 and the "student's" t-test on blank and animal means to check the validity of the results obtained with the micro-Winkler method. There is, however, a certain discrepancy between the results of table 1 and table 2. Why are the QO_2 (w. wt.) water readings of these two spiders significantly greater than the QO_2 (w. wt.) air as shown by analysis in table 7? How can an animal actually absorb more O_2 from water than it normally breathes at rest in air? The answer to this is fairly simple. Oxygen uptake in air will increase in these spiders with the slightest increase in activity as shown by some of the higher results obtained in table 1 when they either spin or perform grooming operations. When the micro-Winkler experiments were performed it was noticed that all spiders were relatively more active than those experimented with in the QO_2 (w. wt.) air determinations. They moved around in the plastic vial trying to find an escape route. It must be remembered that normally these spiders are not truly aquatic and that submergence is only resorted to when trying to escape and when they are flooded perforce by the tides. Thus their normal tendency when submerged and out of their nest is to surface after a while.

Consequently a greater QO_2 (w. wt.) water is simply due to the fact that their respiration rate increases due to increased activity, this leading to a greater uptake of O_2 from water. One might also be tempted to seek an explanation to the higher QO_2 (w. wt.) water by pointing out that small air bubbles inevitably get into the syringe pipette when handling it, as was found to be the case. But this is erroneous as this will also take place when taking a reading at the start of the experiment. When subtracting the initial reading from the one an hour later this will cancel out. It must also be borne in mind that controls were run concurrently.

It is known that temperature will also affect the absorption coefficient of O_2 . This could not have affected the comparison as both QO_2 (w. wt.) air and QO_2 (w. wt.) water were performed at the same temperature, i.e. $17^\circ C$.

The initial explanation is thus the right one.

Having established that both these spiders can absorb O_2 from water when submerged it can be concluded that these spiders use their air film as a physical gill in the same way as aquatic insects described by Ege and Thorpe. It can also be concluded from analysis of tables 1 and 2 that *D. formidabilis* and *A. africanus* have the same QO_2 (w. wt.) air at rest, and that they are equally efficient in the use of their air film when submerged.

From these considerations it is concluded that the comparative efficiency of the air film can affect neither distribution nor zonation of these two spiders.

(ii) Resistance to prolonged immersion.

Why can *D. formidabilis* and *A. africanus* survive for a long period after the collapse of the air film? This may be due to various factors.

Ege (1915) pointed out that the ability to endure the absence of O_2 for short or long periods varies considerably amongst animals and is a common phenomenon among insects. He gives as an example the Dytiscidae which can live 12-24 hours without O_2 . This could be part of the explanation to the long survival period of these spiders after loss of the air bubble, since spiders as a whole are known to withstand O_2 starvation well.

The remaining part of the explanation may come from the anatomical investigations done on *D. formidabilis* and *A. africanus*. When the air film has been completely lost, it must be remembered that air is still present in the booklungs and spiracles. Considering the booklungs first, (see fig. 14 a and b) it is quite possible that the hairs, lining the lips of the booklung slits, prevent water entering the atrium. It is not difficult to see that by leaving these slits open just the right amount, no water will enter the booklungs and yet gaseous exchange will take place here. This in fact is almost like a plastron, but not really so as it will not provide enough O_2 to enable the animal to remain submerged indefinitely. This will only postpone the ultimate end.

Should water enter the epigastric furrow, it is most probable that it would not fill the atrium as this is lined with tiny hydrofuge hairs. It would not seep through to the spaces between the booklung leaves either, as these are very small (not wider than the chitinous projection on the leaves as described earlier) and would thus offer too much surface tension. Gaseous exchange might take place here, but in a less efficient manner as water circulation would be poor. Consider the spiracles and tracheae next. Richards and Korda (1950) state that it is still contentious whether the tracheae of spiders in fact have any respiratory function. Davies and Edney (1952) experimenting on *Lycosa amentata* (Lycosidae), *Meta segmentata*, *Zilla atrica* (all Argyropidae=Epeiridae) and *Tegenaria deuhani* (Agelenidae) found that injection of reduced indigo blue demonstrates that O_2 enters via the tracheae. However they also found that the amount of O_2 taken up is too small to be measured by a standard Warburg manometer and is insufficient to keep the animal alive if the booklungs are blocked. At 30°C they found that intact spiders absorb one-thirtieth of their total O_2 uptake through their spiracle.

Barnes (1966) states: "In some groups, the tracheal tubes are simple and do not extend beyond the abdomen; in others they exceed the booklungs in providing the body with oxygen and extend even into the head and legs. In several small sized groups, the anterior booklungs have also been transformed into tracheae, so that respiration is accomplished entirely by this means." Dissections of the two spiders under consideration has revealed that the tracheae extend into the prosoma and legs of both. Is this significant? Not necessarily. Barnes's statement is a general one and we cannot rely on it to deduce that the tracheae of these spiders have an important respiratory function. Manometric experiments with spiders whose booklungs have been blocked would be necessary. Thus the relative importance of the tracheae after collapse of the air film cannot be established.

Considering the results in table 3 it can be concluded that *D. formidabilis* is able to withstand prolonged submergence only slightly better than *A. africanus*.

However, immersion time becomes unimportant with normal tides and will cancel the above slight discrepancy since:

- both spiders always spin a nest before the tide comes in (see V (b)).
- The nest is watertight and will contain enough oxygen for prolonged immersions.
- The air bubble forms a safety device if the nest should leak.
- The booklungs will tide the spiders over even when the bubble is lost.

Thus immersion will affect neither the zonation nor the distribution of these spiders.

(3) *Desiccation*

Table 4 showed that there is no significant difference between the rates of water loss of these spiders under the same Relative Humidity (0%) at 17°C. It is very doubtful, in any case, that *D. formidabilis* would ever encounter R.H. conditions as low as that used for the experiment in table 4, if it were to invade the territory of *A. africanus*.

One must remember, when considering the effect of desiccation on zonation, that these spiders are terrestrial animals that overcame harsh desiccation perils before they settled in the intertidal zone. They are thus not comparable to marine animals that have not yet overcome this problem. Nevertheless, the desiccation tests were carried out for confirmation. It can be concluded that desiccation is unimportant in determining zonation and that, anyway, the diurnal rhythm of these spiders will keep them out of desiccation hazards.

(4) *Temperature*

Could temperature be one of the factors keeping *D. formidabilis* down? To quote from Kleemola (1963): "Probably, however, the most important cause of the zonal distribution of shore spiders is not the temperature as such. The shore spider fauna are mostly nocturnal. At night the temperature is lower. In the daytime the spiders can burrow themselves into the soil or hide under stones." We have seen that the spiders investigated are nocturnal and usually have their nests well under stones, especially further up the shore. Thus one would be tempted to conclude that temperature could not be a limiting factor. Yet it is felt that such a conclusion might be hasty as borne out by the observations described in IV, c.

The success on land of arachnids as a whole, like that of the insects, depends upon the presence of an epicuticular layer of lipid which prevents the loss of water by evaporation. It is well known that in insects there is a critical t° , characteristic for each species, at which the cuticular wax-layer undergoes a physical change. Above this temperature the rate of water loss by evaporation through the cuticle is very much increased (Wigglesworth 1965). Davies and Edney (1952) and Cloudsley-Thompson (1957) have shown this to be true for the spiders they investigated. It thus seems possible that the cuticle of *D. formidabilis* has a lower critical t° than that of *A. africanus*, but we do not know what these critical temperatures are. Even if we knew them, we would still have to know what are the maximal temperatures experienced in the nests of these 2 spiders, see if there is any difference and finally see if the maximal temperature read in the nest of *A. africanus* is lower or higher than the critical temperature at which the cuticle of *D. formidabilis* loses its efficiency. These considerations do not invalidate our desiccation experiments. These have shown that at 17°C under extreme conditions of desiccation there is no marked difference in water loss. Thus any difference that might occur would have to occur above this temperature.

In the meantime one can only suspect that temperature might be an indirect limiting factor, acting on the rate of water loss, with *D. formidabilis* being dependent on lower temperatures. Diurnal rhythm would on the other hand tend to minimise this effect.

(5) *Humidity*

Nemenz (1955) concludes that all spiders drink when their water deficit becomes great enough and thus they can replace 89-94% of their water loss. Palmgren (1939) and

Nemenz testing preference for various degrees of relative humidity both noted that there is no preference for any particular range, except between very low and high ranges, high ranges being preferred. Chew (1961) found that: "Humidity is probably important only as it interacts with temperature to influence evaporative water loss."

Thus relative humidity should only become an important factor when it is low. Using a paper hygrometer under rocks at "The Island" it was found that there is little difference in R.H. between the various zones. The R.H. was found to be around 85 to 95% in most instances.

Kleemola (1963) states: "It seems that the relative humidity of the air, as important a factor as it may, is not the cause of the zonal distribution of the shore spiders. However, it has been established that moisture in general has a great influence on the distribution of insects and spiders on a shore (e.g. H. Krogerus, Kniille op.c). This moisture must be in the soil as liquid. Water has a cooling effect when evaporating and is also a poor conductor of heat. Therefore it partly levels out the great differences of temperature on the shore and relatively constant circumstances are the result." In the case of our spiders it was found that moisture is abundant in the upper reaches of the intertidal zone as shown by the fact that the undersides of rocks are usually quite wet.

Hence, all in all, conditions of humidity and moisture are unlikely to check a migration of *D. formidabilis* to the upper reaches of the intertidal zone.

(b) THE ROLE OF BIOTIC FACTORS

(1) *Prey preferences*

It was seen in tables 5 and 6 that *D. formidabilis* and *A. africanus* have a selective diet.

Pending further investigations on this aspect, it seems most probable that the availability of prey is a factor controlling the zonation of these two spiders. This would work both ways, in keeping *A. africanus* above H.W.N. and *D. formidabilis* below this level.

(2) *Interspecific competition for nesting sites*

It was shown that *D. formidabilis* is better equipped to compete with *A. africanus* for nesting sites. This is most probably the main factor preventing *A. africanus* from successfully invading the territory of *D. formidabilis* as substantiated by laboratory experiments.

ACKNOWLEDGEMENTS

The work presented in this paper was performed in 1966, while preparing one of several projects for a post-graduate Honours degree at the Zoology Department, University of Cape Town. My grateful thanks must go to the following gentlemen on the staff of the above institution: Professor Day for valuable discussions; Mr. J. Heeg for having agreed to act as my supervisor and for enthusiastic advice; to Dr. A. C. Brown for most appreciated discussions; to Mr. R. I. Dick for having taken the photographs in this paper; to Mr. J. Field for the identification of various Crustacea; to Mr. A. Savage and Mr. N. Fuller for their help in solving technical matters. My thanks must also go to my Honours colleagues for having helped in part of the topographical survey at "The Island," Kommetjie and to Mr. F. Gees of the South African Museum for identifying the scelionid wasp to family

level. Heartfelt thanks are also due to my wife for her help in the survey of "The Island" and her valuable aid in collecting specimens. I am greatly indebted to Mr. B. R. Stuckenberg for reading and offering much knowledgeable advice in the presentation of this paper.

REFERENCES

- BARNES, R. D., 1966. Invertebrate Zoology. *W. B. Saunders Company*, Philadelphia/London.
- BRISTOWE, W. S., 1923. A British semi-marine spider. *Ann. Mag. nat. Hist.* 12 (9): 154.
- , 1930. Notes on the biology of spiders—II Aquatic spiders. *Ann. Mag. nat. Hist.* (10) 6 (33): 343-346.
- , 1958. The world of spiders. *Collins*. St. James Place, London.
- CHEW, R. B., 1961. Ecology of the spiders of desert community. *Jour. New York ent. Soc.* 69: 5-41.
- CLOUDSLEY-THOMPSON, J. L., 1957. Studies in diurnal rhythms: V. Nocturnal ecology and water relations of the British cribellate spiders of the genus *Ciniflo* Bl. *J. Linn. Soc. (Zool.)* 43 (290): 134-152.
- DAVIES, M. E. and EDNEY, E. B., 1952. The evaporation of water from spiders. *J. Exp. Biol.* 29 (4): 571-582.
- EGE, R., 1915. On the respiratory function of the air stores carried by some aquatic insects (Corixidae, Dystiscidae and *Notonecta*) Der Redaktion zugegangen am 20 January 1915. *Zeit. all. Phys.* 17: 81-124.
- FOX, H. M. and WINGFIELD, C. A., 1938. A portable apparatus for the determination of oxygen dissolved in a small volume of water. *J. Exp. Biol.* 15 (3): 437-445.
- GRASSÉ, P. P., (Directeur de publication) 1949. *Traite de Zoologie, anatomie, systematique, Biologie. Onychophore—Tardigrades—Arthropodes—Trilobitomorpes—Chelicerates.* Tome VI. *Masson et Cie*, Paris.
- HALE, L. J., 1958. Biological laboratory Data. *Methuen and Co. Ltd.*, London.
- HEWITT, J., 1915. New South African Arachnida. *Ann. Natal Mus.* 3 (2): 289-328.
- , 1917. Description of new S.A. Arachnida. *Amaurobioides* and others. *Ann. Nat. Mus.* 3 (3): 704. 1919.
- HICKMAN, V. V., 1949. Tasmanian littoral spiders with notes on their respiratory systems, habits and taxonomy. *Pap. Proc. Roy. Soc. Tasmania*, 1948: 31-43.
- , 1951. The identity of spiders belonging to the genus *Amaurobioides* Cambridge. *Pap. Proc. R. Soc. Tasmania*, 1950, 1-2.
- KLEEMOLA, A., 1963. On the zonation of spiders on stony shores of rocky islets in the southwestern archipelago of Finland. *Aquilo* 1: 26-38.
- LAMORAL, B. H., 1968. On the species of the genus *Desis* Walckenaer, 1837, (Araneae: Amaurobiidae) found on the rocky shores of South Africa and South West Africa. *Ann. Natal Mus.*, 20 (1): 139-150, 4 fig., 1 table.
- LAWRENCE, R. F., 1964. A conspectus of S.A. spiders. *Dept. Agr. Tech. Services. Science Bulletin No. 369* (Plant protection series).
- LEHTINEN, P. T., 1967. Classification of the Cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Ann. Zool. Fennici*, 4 (3): 200-468, 516 fig., 8 maps.
- LEVI, H. W., 1967. Adaptations of Respiratory Systems of Spiders. *Evolution*, 21 (3): 571-583.
- MACLEAN, R. C., and IVIMEY COOK, W. R., 1946. Practical field ecology. *George Allen and Unwin Ltd.*, London.
- MASNER, L., 1968. A new Scelionid wasp from the intertidal zone of South Africa (Hymenoptera: Scelionidae). *Ann. Natal Mus.* 20 (1): 195-198, 1 fig.
- MORONEY, M. J., 1965. Facts from figures. *Pelican Books*, A236, London.
- NEMENZ, H., 1955. Über den Wasserhaushalt einiger Spinnen, mit besonderer Berücksichtigung der Transpiration. *Österr. Zool. Zeit.* 5 (123-158).
- NIELSON, E., 1932. The Biology of Spiders. Vol. I *Levin and Munksgaard*, Copenhagen.
- PALMGREN, P., 1939. Ökologische und physiologische Untersuchungen über die spinne *Dolomedes fimbriatus* (Cl.) *Acta Zool. Fenn.* 24 (1-42).
- PANTIN, C. F. A., 1964. Notes on microscopical technique for Zoologists. *Camb. Univ. Press.*, Cambridge.
- POPHAM, E. J., 1954. A new and simple method of demonstrating the physical gill of aquatic insects. *Proc. Roy. Ent. Soc. Lond. (A)* 29: 51-54.
- RICHARDS, A. G. and KORDA, F. H., 1950. Studies on Arthropod cuticle. IV An electron microscope survey of the intima of Arthropod tracheae. *Ann. ent. Soc. Amer.* 43 (1): 49-71.
- SAVORY, T., Arachnida. *Acad. Press.*, Lond. and N.Y.
- TAMBS-LYCHE, H., 1964. A semi-marine spider *Haloteres reprobis* (O.P. Cambridge) in Norway. *Sarsia*. 17: 17-20.
- THORPE, W. H., 1949. Studies on plastron respiration. IV. Plastron respiration in the coleoptera. *Jour. Exp. Biol.* 26 (3): 219-260.

- 1950 Plastron respiration in aquatic insects. *Biol. Rev.* **25**: 344.
- UMBREIT-BURRIS-STAUFFEA, 1959. Manometric Techniques. *Burgess Pub. Co., Minn. U.S.A.*
- WIGGLESWORTH, V. C., 1965. The principle of Insect Physiology. *Methuen and Co. Ltd.* London.
- WOLVEKAMP, H. P. and VLABLON, A. G., 1951-52. Oxygen uptake from water and from air by air-water breathers. *Act. Phys. Pharm. Neerl.* **2**: 214-228.